

Upper Columbia River Steelhead and Spring Chinook Salmon Population Structure and Biological Requirements

Final report, March 2001

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1 Summary

The purpose of this paper is to describe the interim biological requirements for recovery of the Upper Columbia River spring chinook salmon and steelhead Evolutionarily Significant Units (ESUs) currently listed as endangered under the Endangered Species Act (NMFS 1999). The biological requirements we have in mind are the intrinsic features of the ESUs that affect their viability. These features include the number of populations in the ESUs, population size and growth rate, population substructure, and intra- and inter-population diversity. In this paper we do not describe the ecological or environmental conditions that will allow these biological requirements to be met. Where appropriate, in addition to describing the interim biological requirements for recovery, we also provide lower level benchmarks that if crossed indicate varying levels of risk to the ESUs. We expect that these lower benchmarks may be useful in modeling efforts designed to assess the impacts of management actions on the Upper Columbia River ESUs.

One motivation for this paper was the National Marine Fisheries Service's (NMFS) need to make regulatory decisions affecting these ESUs, prior to completion of a formal recovery plan. In particular, two public utility districts proposed a Habitat Conservation Plan to define long-term mid-Columbia River hydropower operations and three federal agencies were consulting with NMFS on lower Columbia River hydropower operations. NMFS, in cooperation with federal hydropower operators, the mid-Columbia public utility districts, and other agencies, established a Quantitative Analytical Report (QAR) process to identify biological requirements of Upper Columbia River steelhead and spring chinook salmon and to analyze the likelihood of meeting those biological requirements, given proposed actions. Two committees were formed through the QAR process, one of which authored this report, and a second conducted simulation modeling to evaluate the likelihood of meeting biological requirements under proposed actions. Names and affiliations of the committee members are listed on the cover of this report. The biological requirements described in this paper are interim.

In this paper, we have generally used the following strategy:

- 1) Identify 'independent populations' (McElhany et al. 2000) of each ESU. If possible, determine what populations were present historically and what populations are present now.
- 2) Determine the intrinsic biological requirements of each population based on the following criteria: abundance, population growth rate, population substructure, and diversity.
- 3) Determine the biological requirements of each ESU in terms of its constituent populations.

Spring chinook salmon interim recovery criteria:

Spring chinook population structure -- We concluded that the weight of the evidence suggests that there are (or historically were) three or four independent populations of spring chinook salmon in the upper Columbia River Basin, inhabiting the Wenatchee, Entiat, Methow, and (possibly) Okanogan River basins. There appears to be considerable population substructure within the Wenatchee and Methow River basins, however, and this population substructure should be considered when evaluating recovery goals and management actions. Spring chinook spawning in Icicle Creek and Leavenworth NFH are an independent population, but this population is not considered part of the Upper Columbia spring chinook ESU (NMFS 1999).

Number of independent spring chinook populations -- We suggest that a reasonable interim recovery level is at least three independent, viable populations, one each in the Wenatchee, Entiat and Methow River basins. The Okanogan River has apparently not supported a spring chinook population since at least the 1930's, so we see little point in setting interim recovery goals for this potential population at this time. Rather, we suggest deferring discussion of goals for the spring chinook in the Okanogan River basin to an Upper Columbia River recovery team.

Having at least three populations will reduce the probability that a single catastrophic event could cause the extinction of the entire ESU. Multiple populations within an ESU will also increase the likelihood that a diversity of phenotypic and genotypic characteristics will be maintained. This will allow for the operation of natural evolutionary processes important for the long-term persistence of the ESU.

Spring chinook population abundance -- We pursued several strategies for obtaining interim recovery abundance levels. First, we reviewed the historical record to determine the abundance of the populations during times when they were considered to be relatively healthy. Accurate abundance estimates for Upper Columbia salmonid populations are only available for approximately the last 50 years, although Mullan et al. (1992) attempted to roughly estimate salmonid abundance in the Upper Columbia prior to large-scale European immigration. Second, we attempted to estimate the current carrying capacity of the Upper Columbia tributaries, and compared these to estimates of what the capacity might have been historically. Third, we used results from population modeling to determine population abundance levels that would result in a low risk of extinction. For the current document we used very general modeling results drawn from the conservation biology literature. We expect more detailed, population-specific modeling to occur at a later time.

The stated purposes of the ESA are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, to provide a program for the conservation of such endangered species and threatened species, and to take such steps as may be appropriate to achieve these purposes (ESA sec. 2(b)). The ESA's focus is, therefore, on natural populations and the ecosystems upon which they depend. Artificial propagation of a listed salmonid species is therefore not a substitute for eliminating the factors causing or contributing to a species' decline (Hard et al. 1992). In order to satisfy these objectives of the ESA, all of the abundance criteria discussed below apply to natural-origin spawners, which are defined as the progeny of fish that spawned in the wild.

In all cases abundance must be measured over a period of several salmon generation (8-16 years) to confident that the interim abundance criteria are indeed met (see section 4.2 and Appendix D).

Wenatchee River population: We recommend an interim recovery abundance level for the Wenatchee River population of 3750 naturally produced spawners/year, a value that falls within the range of the habitat capacity estimates, historical run sizes, and simple PVA recommendations.

Entiat River population: We recommend an interim recovery abundance level for the Entiat River population of 500 naturally produced spawners/year. This value does not fall within the range of the simple PVA recommendations, but is consistent with the estimated current and historical habitat capacity and historical run sizes. In this report, we have not attempted to quantify the capacity of the Entiat River watershed under improved habitat conditions. NMFS et al. (1998) describe numerous potential habitat improvement strategies that for the Entiat River watershed, so the final recovery goals for the Entiat River spring chinook population may be larger than the interim goal recommended here.

Methow River population: We recommend an interim recovery abundance level for the Methow River population of 2000 naturally produced spawners/year, a value that falls within the range of the habitat capacity estimates, historical run sizes, and simple PVA recommendations.

The committee decided that it would be useful to identify an abundance level below which demographic, genetic, and other risk factors to the populations become of increasing concern, and uncertainties in production response become magnified. These levels (one for each population) were determined primarily from the lower end of the spawning abundances exhibited by the Upper Columbia populations during the time period when they were considered to be relatively healthy. We set the cautionary abundance levels for the Wenatchee, Entiat, and Methow River spring chinook salmon populations to be 1200, 150, and 750 spawners per year, respectively.

Spring chinook population growth rates -- In order to be considered recovered, a population must have a geometric mean NRR significantly greater than 1.0. This means that in order to be considered recovered,

the populations must be growing. In the long term (after recovery is complete), a stable population without hatchery straying is expected to have a geometric mean NRR of 1.0.

Spring chinook population substructure -- Qualitative criteria that apply to all populations: In order to be considered recovered, spring chinook populations should be able to utilize properly functioning habitat in multiple spawning streams within each major tributary, with patterns of straying among these areas free from human-caused disruptions.

Quantitative criteria:

Wenatchee River population: Averaged over 12 years, Wenatchee River spring chinook should spawn in at least three streams within the Wenatchee River Basin, with each stream containing at least 5% of the total spawning abundance.

Methow River population: Averaged over 12 years, Methow River spring chinook should spawn in at least three streams within the Methow River Basin, with each stream containing at least 5% of the total spawning abundance.

Entiat River: No quantitative criteria.

Spring chinook diversity -- The Upper Columbia River spring chinook populations must be naturally self-sustaining and not dependent on artificial propagation. Levels of gene flow from out-of-ESU hatchery stocks into natural Upper Columbia spring chinook populations should be less than 1% (McElhany et al. 2000), and patterns of straying and gene flow among the natural populations should be free from human-caused alterations.

Steelhead interim recovery criteria

Steelhead population structure -- A complete understanding of the historical population structure of Upper Columbia steelhead appears impossible to achieve. However, based primarily on current and historical spawning distributions and the assumption of reasonably accurate homing rates, we believe that historically there were at least three (possibly four) major populations of steelhead in the Upper Columbia River area, one each in the Wenatchee, Entiat, Methow and (possibly) Okanogan River Basins. Due to lack of detailed data on spawning locations and straying patterns, the very limited nature of the existing genetic data, and long history of extensive artificial propagation of Upper Columbia River steelhead, it is impossible rule out the possibility that one of more of these major tributaries could have historically contained more than one independent population.

Since the late 1960's (and perhaps since the 1940's), steelhead in the Upper Columbia River area may have been functionally part of just a single population, due to very large scale supplementation from a common hatchery subpopulation. The existing genetic data are consistent with this conclusion, but they do not rule out the possibility that independent populations have persisted despite large scale supplementation. Even if large scale supplementation has resulted in a single independent population, this does not preclude multiple independent populations from existing in a recovered ESU.

Number of steelhead populations -- We suggest that a reasonable interim recovery level is three independent, viable populations, one each in the Wenatchee, Entiat and Methow Rivers basins. It is possible that the final recovery goals will also require a population of steelhead in the Okanogan, but we defer discussion of goals for steelhead in the Okanogan to an Upper Columbia River recovery team.

Having at least three populations will reduce the probability that a single catastrophic event could cause the extinction of the entire ESU. Multiple populations within an ESU will also increase the likelihood that a diversity of phenotypic and genotypic characteristics will be maintained. This will allow for the operation of natural evolutionary processes important for the long-term persistence of the ESU.

We emphasize that even if past management actions have resulted in the creation of a single Upper Columbia River steelhead population, this does not preclude a recovered ESU from containing multiple independent populations. The population definition we are using in the document is based on demography, not genetics. This means that even if genetic differences between historical steelhead populations have been lost due to the GCFMP and subsequent large-scale artificial propagation programs, this loss of diversity does not preclude groups of steelhead from becoming demographically independent in the future. In fact, this process has already begun with the creation of a separate steelhead supplementation program for the Wenatchee River. Over time, demographically independent populations will diverge genetically to a greater or lesser degree, depending on the size of each population, the rate of gene flow among the populations, and degree to which local ecological differences select for alternative genotypes in each population.

Steelhead population abundance -- In recommending interim recovery abundance levels for Upper Columbia steelhead, we used the same approach as we used for spring chinook salmon. Note that although we have provided interim recovery abundance levels for each population, we recognize that it may not be possible to accurately estimate spawning abundance at the scale of individual populations. As we discussed earlier, native non-anadromous *O. mykiss* that spawn in Upper Columbia areas accessible to anadromous fish are considered part of the same biological ESU as Upper Columbia steelhead (Busby et al. 1996). Due to considerable uncertainty about the demographic relationships between resident and anadromous fish, however, we have not included resident fish in any of the spawning abundance levels we discuss below.

Wenatchee and Methow River populations - We recommend an interim recovery abundance level of ~2500 naturally produced spawners each for the Wenatchee and Methow Rivers. These abundance levels fall within a range defined by reasonable combinations of estimated smolt production capacities and smolt/spawner ratios, historical production levels and general conservation guidelines.

Entiat River population - We recommend an interim abundance recovery level for the Entiat River population of ~500 naturally produced spawners. This is considerably below the general conservation guidelines of several thousand spawners, but is consistent with estimates of current and historical habitat capacity.

Steelhead population growth rate -- In order to be considered recovered, an Upper Columbia steelhead population must have a geometric mean NRR significantly greater than 1.0, measured over 12 brood cycles. We did not attempt to use the past variance in estimated NRR as an indicator of the likely future variance (like we did for spring chinook) because the demographic history of these populations has been so dominated by artificial propagation that the assumption that the future variance in NRR will be similar to the past is untenable. We chose 12 brood cycles as a reasonable value over which to measure the NRR because this roughly corresponds to two complete Upper Columbia steelhead generations, and is consistent with the range of time frames suggested by the spring chinook salmon uncertainty analyses (Section 4.2 and Appendix D).

The criterion above assumes that the population will grow from a small size to its recovery level without substantial supplementation. Another scenario (perhaps more realistic for Upper Columbia River steelhead) that might lead to recovery would be to increase the population's size artificially via supplementation, and then stop supplementing when the population is large. If the population sustains itself after supplementation ceases, the population's geometric mean NRR would be equal to ~1 (after supplementation), but might never be significantly greater than 1. Under this scenario, a reasonable interim recovery criteria might be to require that the population's geometric mean NRR not be significantly less than 1.0, with the geometric mean calculated over a sufficient number of years to achieve a desired level of statistical power.

Steelhead population substructure -- In order to be considered recovered, Upper Columbia steelhead populations should be able to utilize properly functioning habitat in multiple spawning streams within each major tributary, with patterns of straying among these areas free from human-caused disruptions. At this

time, we do not believe that there is sufficient information on Upper Columbia steelhead spawning distributions to recommend any quantitative criteria for spawning distributions within each major tributary.

Steelhead diversity -- The Upper Columbia River steelhead populations must be naturally self-sustaining and not dependent on artificial propagation. Levels of gene flow from out-of-ESU hatchery stocks into natural Upper Columbia steelhead populations should be less than 1%, and patterns of straying and gene flow among the natural populations should be free from human-caused alterations.

2 Introduction

The purpose of this paper is to describe the interim biological requirements for recovery of the Upper Columbia River² spring chinook salmon and steelhead Evolutionarily Significant Units (ESU) currently listed as endangered under the Endangered Species Act (NMFS 1999). The biological requirements we have in mind are the intrinsic features of the ESUs that affect their viability. These features include the number of populations in the ESUs, population size and growth rate, population substructure, and intra- and inter-population diversity. In this paper we do not describe the ecological or environmental conditions that will allow these biological requirements to be met. Where appropriate, in addition to describing the interim biological requirements for recovery, we also provide lower level benchmarks that if crossed indicate varying levels of risk to the ESUs. We expect that these lower benchmarks may be useful in modeling efforts designed to assess the impacts of management actions on the Upper Columbia River ESUs.

One motivation for this paper was the National Marine Fisheries Service's (NMFS) need to make regulatory decisions affecting these ESUs, prior to completion of a formal recovery plan. In particular, two public utility districts proposed a Habitat Conservation Plan to define long-term mid-Columbia River hydropower operations and three federal agencies were consulting with NMFS on lower Columbia River hydropower operations. NMFS, in cooperation with federal hydropower operators, the mid-Columbia public utility districts, and other agencies, established a Quantitative Analytical Report (QAR) process to identify biological requirements of Upper Columbia River steelhead and spring chinook salmon and to analyze the likelihood of meeting those biological requirements, given proposed actions. Two committees were formed through the QAR process, one of which authored this report, and a second conducted simulation modeling to evaluate the likelihood of meeting biological requirements under proposed actions. Names and affiliations of the committee members are listed on the cover of this report. The biological requirements described in this paper are interim.

In this paper, we have generally used the following strategy:

- 4) Identify 'independent populations' (see below) of each ESU. If possible, determine what populations were present historically and what populations are present now.
- 5) Determine the intrinsic biological requirements of each population based on the following criteria: abundance, population growth rate, population substructure, and diversity.
- 6) Determine the biological requirements of each ESU in terms of its constituent populations.

3 Identifying independent populations

Definition - By an *independent population*, we mean an aggregation of one or more local breeding units (demes) that are closely linked by exchange of individuals among themselves, but are isolated from other independent populations to such an extent that exchanges of individuals among the independent populations do not appreciably affect the population dynamics or extinction risk of the independent populations over a 100-year time frame. Thus we are defining populations as units about which it is

² In the coastwide status reviews for steelhead and chinook salmon (Busby et al. 1996; Myers 1998), steelhead spawning upstream of the mouth of the Yakima River and stream-type chinook salmon spawning upstream of Rock Island Dam were considered to be in the Upper Columbia River steelhead and spring-run chinook salmon ESUs, respectively. This same geographic region has often been referred to as the Mid-Columbia River area (Chapman et al. 1995; Chapman et al. 1994; Mullan et al. 1992). Since this report is concerned with biological requirements for ESA listed species, we will follow the "Upper Columbia River" terminology in order to be consistent with the names assigned to the listed ESUs in this area.

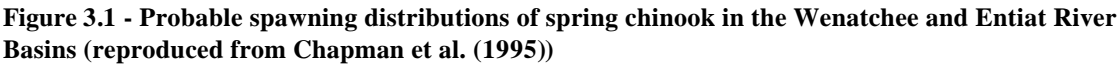
biologically meaningful to evaluate and discuss the extinction risk due to factors such as demographic, genetic or local environmental stochasticity of one population independently from other populations. This focus on demographic independence in defining populations is consistent with how the population concept is often applied in fisheries analysis and population viability modeling. For example, many commonly used spawner-recruit models explicitly or implicitly assume reproductive isolation among populations. The exact level of reproductive isolation that is required for a population to have substantially independent dynamics is not well understood, but some theoretical work suggests that substantial independence will occur when the proportion of a population that consists of migrants is less than about 10% (Hasting 1993).

Identifying independent populations – Identifying independent populations requires estimating the level of reproductive isolation among fish spawning in different areas or times. We used the following types of data to gain insight into the degree of reproductive isolation among spawners in different areas: 1) geographic spawning distributions, 2) correlations in abundance over time, 3) patterns of allozyme allele frequencies, 4) physical data on the environments inhabited by the fish, 5) patterns of morphological variation of fish spawning in different areas, and 6) mark/recapture data. Allele frequency data can be used to test models of population structure and to estimate migration rates among groups. Abundance correlations can be used to directly test for demographic independence. Geographic and temporal spawning distributions can be used to make judgements on the likelihood of straying among areas. Mark/recapture data can provide direct estimates of straying, and environmental data can be used to make judgements on the likelihood of local adaptations among groups. Each of these will be discussed in greater detail below.

3.1 Current and historical spawning distributions

3.1.1 Spring chinook salmon spawning distributions

Mullan et al. (1992) and Chapman et al. (1995) summarize current and historical spawning distributions for spring chinook salmon in the Wenatchee, Entiat, Methow and Okanogan River basins (Figures 2.1 and 2.2, reproduced from Chapman et al. (1995)). Within the Wenatchee River Basin, Chapman et al. (1995) listed (in order of importance) the Chiwawa River, Nason Creek, Little Wenatchee and White Rivers as the primary spring chinook spawning areas. Spring chinook also spawn in Icicle Creek, but currently these spawners are believed to be primarily returns from Leavenworth Hatchery (Chapman et al. (1995); see also Appendix C). Some spring chinook also spawn in Peshastin Creek. Within the Methow River Basin, Chapman et al. (1995) list in order of importance the mainstem Methow, Twisp, Chewuch and Lost Rivers as the primary spring chinook spawning areas. Spring chinook also spawn in the mainstem Entiat River and lower part of the Mad River. In the 1930's, spring chinook were observed spawning in parts of the Okanogan River Basin but have not been observed in the Okanogan system since then (Chapman et al. 1995). With the possible exception of the Okanogan River, the approximate spawning distributions of spring chinook in the Upper Columbia River area are believed to be similar to what they were historically (Mullan et al. 1992). Major discontinuities in the spawning distributions that might lead to some level of demographic isolation include sections of the mainstem Columbia River between the major tributaries and the lower mainstem areas of each major tributary. Tumwater Canyon and Lake Wenatchee are smaller discontinuities within the Wenatchee River watershed (Figures 2.1 and 2.2).



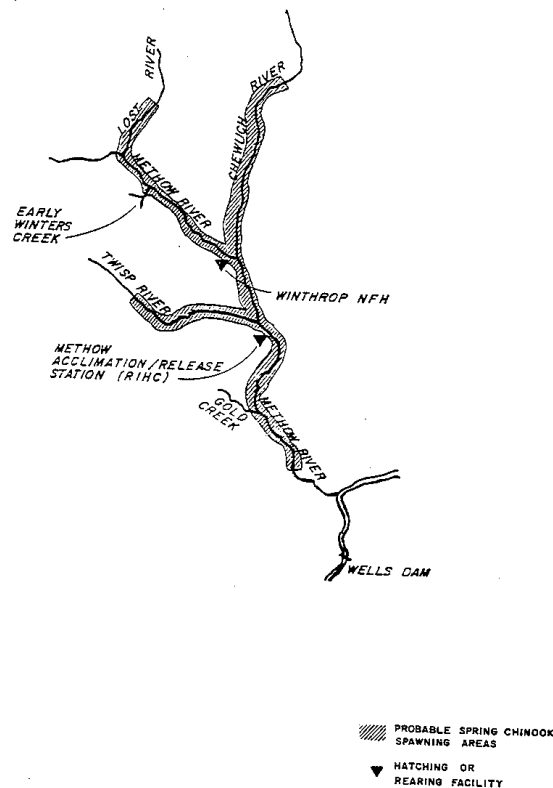


Figure 3.2 - Probable spawning locations of spring chinook salmon in the Methow River Basin (reproduced from Chapman et al. (1995))

3.1.2 Steelhead spawning distributions

Mullan et al. (1992) and Chapman et al. (1994) summarized the available information on historical and current spawning distributions of steelhead in the Upper Columbia River. The conclusions from these summaries were that steelhead used all the major tributaries in the Upper-Columbia River area, and that Fulton (1970) had concluded that the (then) current spawning distributions were similar to what they had been historically. The data summarized by these reviews suggest four disjunct spawning areas: the Wenatchee River and tributaries, the Entiat River and tributaries, the Methow River and tributaries, and parts of the Okanogan River and tributaries (Figures 2.3 and 2.4, reproduced from Chapman et al. (1994)). These streams enter the mainstem Columbia River at RM 468, 484, 524, and 534, respectively. Once the fish enter these streams, they may travel 75 miles or more to spawning areas. Thus, geographic separation of spawning groups is likely between the subbasins. Various studies of straying in Pacific salmon suggest that straying among rivers the size of the Wenatchee, Entiat, Methow and Okanogan is often low (reviewed by Quinn et al. (1991)). Detailed information on steelhead spawning locations within the Upper-Columbia River tributaries is lacking due to the difficulty of observing spawning steelhead in these areas (Chapman et al. 1994; Fulton 1970; Mullan et al. 1992). Major discontinuities in the spawning distributions that might lead to some level of demographic isolation include sections of the mainstem Columbia River between the major tributaries (Figures 2.3 and 2.4).

Figure 3-3 Steelhead spawning areas in the Wenatchee and Entiat River Basins (reproduced from Chapman et al. (1994))

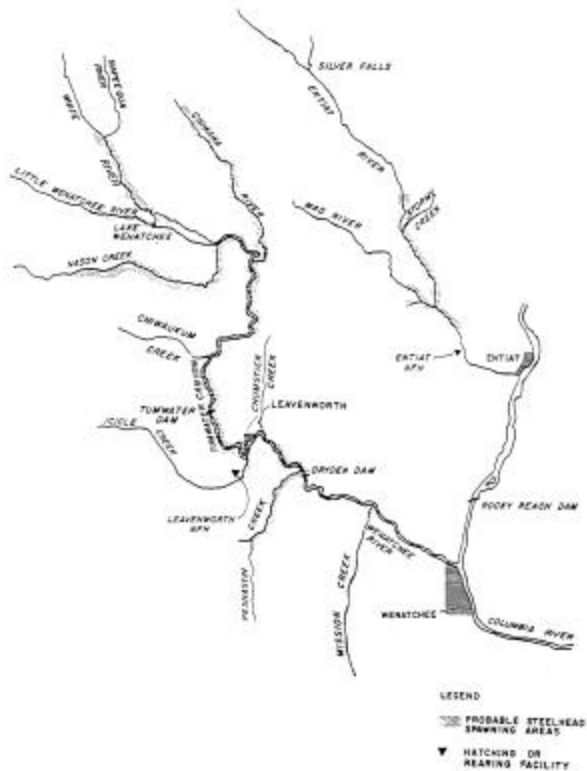
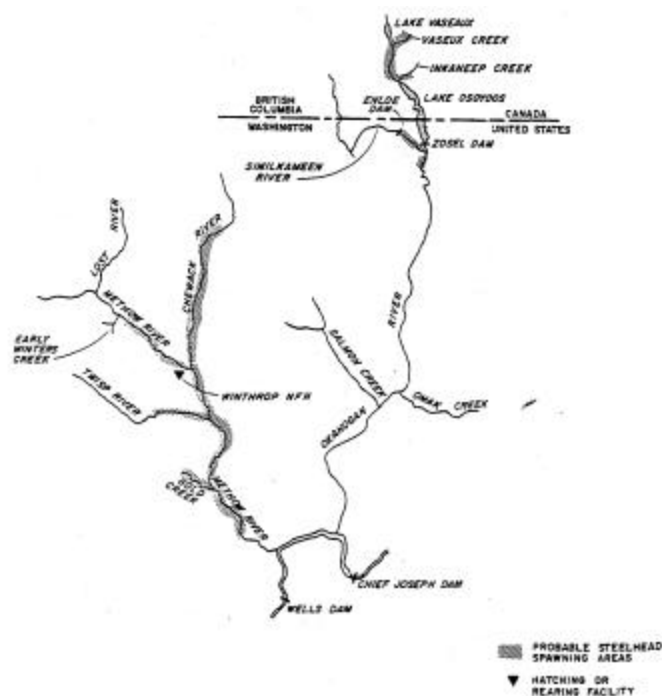


Figure 2.4 - Steelhead spawning areas in the Methow and Okanogan River Basins (reproduced from Chapman et al. 1994)



3.2 Abundance correlations and demographic history

3.2.1 Spring chinook salmon correlations and history

History: From 1939 to 1943, all spring chinook adults passing upstream of Rock Island Dam were collected and either planted into Nason Creek, the Entiat River or Methow River or spawned in hatcheries with subsequent release of their progeny into these areas (reviewed by Chapman et al. 1995; Mullan et al. 1992; Myers 1998). This probably had the effect of genetically homogenizing any existing spring chinook population structure in these areas, especially since in the years prior to 1938 spring chinook populations in the area were extremely depressed (Fish and Hanavan 1948; Mullan et al. 1992). Since 1943, hatchery releases of spring chinook have occurred periodically (and regularly since the 1970's) in the Wenatchee, Entiat and Methow River Basins. Except for the Rock Island and Methow Hatchery programs that began in the late 1980's, Upper Columbia River hatchery populations are believed to have been substantially demographically isolated from naturally spawning populations of spring chinook in the Upper Columbia River area (Chapman et al. 1995).

Abundance correlations:

Examining correlations in abundance may provide some insight into demographic links among spawning areas (e.g. Rieman and McIntyre 1996). Spawning areas could have correlated abundance due to both demographic and environmental factors, so in order to use abundance correlations as measure of demographic connectedness it is necessary to be able to rule out correlated environments as a causal factor. This will usually be impossible to do satisfactorily, so these analyses need to be used cautiously when drawing inferences about population structure.

As a measure of relative abundance in each spawning area, we used unexpanded redd count data from index areas (Appendix A) from the late 1950's to 1998. The index areas surveyed have remained the same over this time period (C. Peven, per. com.). Redd counts in many of the index areas are significantly correlated (Table 2.1). Two exceptions to the pattern of high correlations are counts in the Icicle Creek and Upper Wenatchee areas. Redd counts in Icicle Creek were not significantly correlated with counts in any other area, and counts in the Upper Wenatchee were significantly correlated with counts in only two other areas. Spring chinook that spawn in Icicle Creek are heavily influenced by returns from Leavenworth Hatchery (see section on straying below), which may explain the lack of correlation of counts in this stream with other areas.

Many of the index areas have declining trends (Appendix A), and these common trends may partly explain the generally high correlations among areas. Because these trends probably reflect common environmental factors (e.g. dams, ocean conditions), we attempted to statistically remove these trends from the data. We tried several data transformations, and found that the transformation $\ln(N_t + 1) - \ln(N_{t-1} + 1)$ was most effective at detrending the data (L. Holsinger, per. com., Appendix A). Correlations among the detrended counts remained generally high, but the patterns of correlations differed substantially from the raw correlations (Table 2.2). For example, although the detrended counts in Icicle Creek remained uncorrelated with all other counts, the detrended counts in the Upper Wenatchee were positively correlated with all other areas except Icicle Creek. In order to better visualize correlations among locations, we used the detrended correlation matrix to construct a cluster diagram using the UPGMA method (Figure 2.5). This diagram shows that index counts from pairs of index areas within the same major tributary tend to be slightly more correlated than counts from pairs of populations from a different major tributary. This pattern could be due to greater environmental correlations within than among tributaries or higher rates of straying within than among tributaries, or could simply be due to chance.

Summary: Redd counts in many of the index areas are positively correlated, but it is not clear if this is due to common environmental factors, high migration among areas, or a combination of both. The abundance

correlations provide some support for population structure at the level of the major tributaries (Figure 2.5). The Icicle Creek redd counts are uncorrelated with counts in other areas, possibly because of the strong demographic influence of Leavenworth NFH, isolation from upriver spawning areas by Tumwater Canyon, or a combination of both of these factors.

Table 2.1 - Pearson correlation coefficients between spring chinook salmon redd counts from different locations

	Methow	Chewack	Twisp	Lost	Entiat	Nason	Little Wenatchee	White	Chiwawa	Icicle	Upper Wenatchee
Methow	1.00	0.45	0.82	0.87	0.70	0.68	0.73	0.17	0.61	0.12	0.14
Chewack	0.45	1.00	0.71	0.36	0.59	0.46	0.30	0.28	0.43	0.22	0.36
Twisp	0.82	0.71	1.00	0.67	0.86	0.87	0.61	0.21	0.59	0.23	0.13
Lost	0.87	0.36	0.67	1.00	0.62	0.59	0.78	0.17	0.71	0.00	0.13
Entiat	0.70	0.59	0.86	0.62	1.00	0.78	0.65	0.24	0.60	0.22	0.00
Nason	0.68	0.46	0.87	0.59	0.78	1.00	0.72	0.30	0.72	0.16	0.06
Little Wenatchee	0.73	0.30	0.61	0.78	0.65	0.72	1.00	0.54	0.88	0.11	0.26
White	0.17	0.28	0.21	0.17	0.24	0.30	0.54	1.00	0.53	0.13	0.64
Chiwawa	0.61	0.43	0.59	0.71	0.60	0.72	0.88	0.53	1.00	-0.04	0.28
Icicle	0.12	0.22	0.23	0.00	0.22	0.16	0.11	0.13	-0.04	1.00	-0.05
Upper Wenatchee	0.14	0.36	0.13	0.13	0.00	0.06	0.26	0.64	0.28	-0.05	1.00

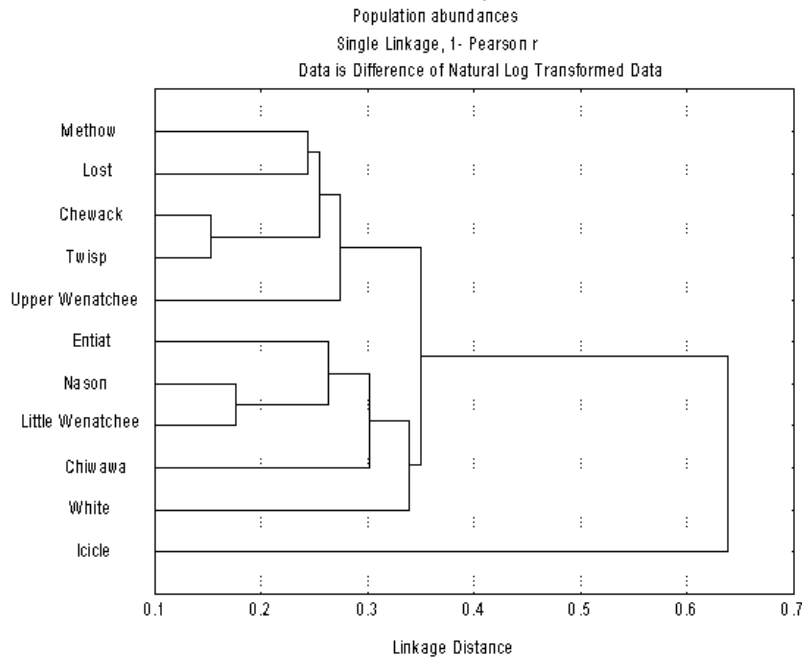
bold values are significant at the 5% level or better

Table 2.2 - Pearson correlation coefficients between detrended spring chinook salmon redd counts from different locations

	Methow	Chewack	Twisp	Lost	Entiat	Nason	Little Wenatchee	White	Chiwawa	Icicle	Upper Wenatchee
Methow	1.00	0.52	0.75	0.76	0.31	0.27	0.43	0.29	0.22	0.34	0.55
Chewack	0.52	1.00	0.85	0.46	0.53	0.49	0.44	0.23	0.58	0.36	0.61
Twisp	0.75	0.85	1.00	0.56	0.58	0.65	0.61	0.46	0.47	0.32	0.73
Lost	0.76	0.46	0.56	1.00	0.47	0.36	0.64	0.32	0.47	0.21	0.50
Entiat	0.31	0.53	0.58	0.47	1.00	0.70	0.74	0.40	0.57	0.24	0.46
Nason	0.27	0.49	0.65	0.36	0.70	1.00	0.82	0.66	0.54	0.01	0.56
Little Wenatchee	0.43	0.44	0.61	0.64	0.74	0.82	1.00	0.62	0.70	0.04	0.57
White	0.29	0.23	0.46	0.32	0.40	0.66	0.62	1.00	0.20	0.14	0.58
Chiwawa	0.22	0.58	0.47	0.47	0.57	0.54	0.70	0.20	1.00	-0.18	0.40
Icicle	0.34	0.36	0.32	0.21	0.24	0.01	0.04	0.14	-0.18	1.00	-0.05
Upper Wenatchee	0.55	0.61	0.73	0.50	0.46	0.56	0.57	0.58	0.40	-0.05	1.00

bold values are significant at the 5% level or better

Figure 2.5 - UPGMA cluster diagram using the detrended correlation coefficients among spring chinook redd counts as an index of identity



3.2.2 Steelhead demographic history

We do not know of any direct data on spawning abundance or stray rates for the individual tributaries in the Upper Columbia River area. The total abundance of steelhead passing Rock Island Dam has generally increased since records began in 1933 (Chapman et al. 1994), but Mullan et al. (1992) and Chapman et al. (1994) describe several management actions that probably have substantially influenced the population structure of Upper Columbia River steelhead. First, the Grand Coulee Fish Maintenance Project (GCFMP, Fish and Hanavan 1948) probably resulted in substantial mixing of steelhead from all areas upstream of Rock Island Dam. This mixing was probably not complete because non-anadromous and 5+ year old anadromous *O. mykiss* were not trapped. After the GCFMP, extensive artificial propagation of steelhead in the Upper Columbia area resumed in the 1960's (Chapman et al. 1994). Steelhead smolts resulting from broodstock trapped at either Priest Rapids or Wells Dams have been extensively planted throughout the Wenatchee, Entiat and Methow Rivers. At least since the 1985/86 cycle, between 71% and 90% of the steelhead that passed Priest Rapids Dam were hatchery produced (see section 4.2). These factors suggest that at least since the late 1960's or 1970's all steelhead in the Wenatchee, Entiat and Methow (and Okanogan?) may have been part of a single independent population, with the hatcheries as the primary source of productivity. More recently, separate hatchery programs have been developed for the Wenatchee and Methow Rivers. Hence there are now at least two potentially demographically independent populations of steelhead in the Upper Columbia River area.

These tentative conclusions must be tempered by two points, however. First, several studies have suggested that hatchery produced steelhead may not be as successful at reproducing in the wild as are wild steelhead (Leider et al. 1990; Reisenbichler 1997; Reisenbichler and McIntyre 1977). If hatchery produced steelhead spawning naturally in Upper-Columbia tributaries are much less successful at producing offspring than their wild counterparts, then the demographic and genetic contributions of hatchery fish to these wild spawning areas could be much less than would be predicted from the total proportion of naturally spawning hatchery fish. For example, under the extreme assumption that naturally spawning hatchery fish produce no returning adult progeny, then naturally spawning steelhead in different tributaries could be reproductively isolated despite the high proportion of common-origin hatchery-produced fish spawning in the same tributaries.

The second important point to consider is the relationship between anadromous and resident *O. mykiss* (steelhead and rainbow trout). Mullan et al. (1992) concluded that steelhead pursue alternative anadromous or resident strategies depending on local environmental conditions, and that anadromous and resident *O. mykiss* interbreed and can be part of the same demographic population. In their status review of West Coast steelhead, Busby et al. (1996) concluded that, in general, steelhead ESUs include native resident *O. mykiss* in areas where they can interbreed, and mentioned the Upper Columbia River as an area in which the role of resident fish may be particularly important. If native resident fish are "counted" as part of the natural component(s) of the Upper Columbia River steelhead population(s), this would have the effect of increasing the apparent wild:hatchery ratio and could suggest that demographically independent populations of *O. mykiss* could persist in the different tributaries despite the large-scale steelhead hatchery programs. At this time, however, there are insufficient data to effectively evaluate the demographic importance of resident *O. mykiss* to Upper Columbia steelhead populations.

3.3 Genetic data

3.3.1 Spring chinook salmon genetic data

WDFW has an extensive allozyme data set of spring chinook sampled from the Wenatchee, Entiat, and Methow River Basins, consisting of 1269 individuals that have been aged and scored for 44 allozyme loci. In order to gain insight into the population structure of Upper Columbia spring chinook, we performed several types of analyses. For most of these analyses, we divided the sample up into 27 broodyear by sampling locality combinations, after eliminating locality/broodyear combinations with sample sizes of less than 10 individuals (Table 2.3). For some analyses we also eliminated locality/broodyear combinations with sample sizes of less than 25 individuals. Breaking the sample down by broodyears allowed us to make inferences about genetic differences among spawning areas after taking into account the level of variation among broodyears within localities. These analyses are discussed in detail below.

Cluster analyses: We used several clustering methods to visualize patterns of a genetic differentiation among sampling sites. A typical clustering diagram is shown in Figure 2.6, which shows a neighbor-joining tree of the locality by broodyear samples, based on Nei's unbiased genetic distance (Nei 1987).

Table 2.3 - Locality - Broodyear samples used in analyses

Location- Broodyear	sample size
Chewack 87	10
Chewack 88	88
Chewack 89	35
Chewack 92	37
Chewack 93	18
Chiwawa 84	29
Chiwawa 85	33
Chiwawa 86	14
Chiwawa 87	23
Chiwawa 88	76
Chiwawa 89	27
Chiwawa 92	11
Methow 88	36
Methow 89	52
Methow 92	38
Nason 85	20
Nason 87	15
Nason 88	40
Nason 89	17
Twisp 88	75
Twisp 89	18
Twisp 92	29
White 84	20
White 85	31
White 87	22
White 88	27
White 89	14

Figure 2.6 - UPGMA cluster diagram of all broodyear-locality samples with a sample size of 25 or greater.



The numbers by the internal nodes in the tree in Figure 2.6 refer to the percentage of times that node appeared in 1000 bootstrap replicates (bootstrapping over loci). This tree is representative of a large number of trees that we generated, using different subsets of the whole data set (e.g., removing known hatchery strays, or changing the minimum sample size threshold). In general, these cluster analyses showed little evidence of geographic structure, and in many cases broodyears from the same sampling locality did not cluster together. Two exceptions to this pattern were samples from the White and Twisp Rivers. Samples from these two areas tended to be consistently distinct, and broodyears from each of these areas tended to form clusters with high (White River) or moderate (Twisp River) bootstrap support values (Figure 2.6).

Pairwise differences in allele frequencies:

A simple way to determine if observed allele distributions from different groups were drawn from the same underlying distribution is to perform contingency table tests (Weir 1996, p. 163). These statistical tests can be used to test the null hypothesis that two observed samples of alleles were randomly drawn from the same infinitely sized population without replacement, or the same finite sized population with replacement (see Waples 1998 and discussion in steelhead section). All of the spring chinook used in these analyses were aged and assigned to a broodyear, so it is possible to statistically test if samples from two areas are different without confounding temporal and spatial differences. Table 2.4 shows the results of 20 contingency tests (log likelihood G-tests – Sokal and Rohlf 1981) among samples from different locations but the same broodyear. The denominator in each table entry is the number of broodyears sampled for each pair of geographic locations, and the numerator is the number of tests that were significant at the 5% level or better (not corrected for multiple tests). The pattern of statistical significance in Table 2.4 is similar to what was seen in the cluster analyses (Figure 2.6). Four of six tests involving the White River samples and all six of the tests involving the Twisp River sample were significant. This compares to two significant tests out of nine that involved only the Chewuch, Chiwawa, Methow or Nason Rivers .

Table 2.4 – Number of significant ($p < 0.05$ or better) contingency tests/total number of contingency tests among the same broodyears from different localities.

	Chewuch	Chiwawa	Methow	Nason	Twisp	White
Chewuch		0/1	1/3	1/1	2/2	1/1
Chiwawa			0/2	0/1	1/1	2/2
Methow				0/1	1/1	0/1
Nason					1/1	0/1
Twisp						1/1
White						

The results of the contingency analyses show that not all of the samples were drawn randomly from the same group, even after taking into account differences among broodyears. In particular, the White and Twisp River samples are clearly statistically different from each other and many of the other samples. The biological significance of these differences (i.e., whether they are large enough to suggest that, for example, the White and Twisp River samples were drawn from different independent populations) will be discussed further below.

Analysis of genetic variance:

A useful way to summarize genetic variation is to use a hierarchical approach to partition observed genetic variation into different components (Weir 1996). These results can be used directly to describe the geographic and/or temporal scale of population (sub)structure, and also be used to estimate model parameters such as the level of gene flow or time of divergence among populations. In the case of Upper Columbia spring chinook salmon, we partitioned the observed variance in allozyme allele frequencies among the samples listed in Table 2.3 into three components (Table 2.5): among broodyears within sampling locality; among sampling localities within major tributaries; and among major tributaries (the

major tributaries in this analysis are the Methow and Wenatchee Basins; there was insufficient data to include the Entiat River Basin). Under this hierarchy, there are significant differences among broodyears within localities, and among localities within major tributaries, but there is no significant component of variation among the major tributaries. Similar results were obtained if only samples with 25 or more individuals were included, or if known stray hatchery fish were excluded (data not shown).

Table 2.5 - Hierarchical analysis of genetic variation

	Among major tribs (F_{TP})	Among spawning areas, within major tribs (F_{ST})	Among broodyears, within spawning areas (F_{YS})
point estimate	0.001859	0.012339	0.016846
95% confidence interval	0.006257 -0.002656	0.016595 0.007308	0.020351 0.012877

From the cluster analyses, only the samples from the White and Twisp Rivers appeared to be consistently genetically distinct across multiple broodyears (Figure 2.6). In order to determine if the significant component of among spawning area genetic variance was due mostly to these two areas, we repeated the hierarchical analysis with samples from the White and Twisp Rivers excluded (Table 2.6). Consistent with the cluster analyses, the samples from the White and Twisp Rivers appear to contribute the majority of the variation observed among localities, although even without these samples significant differences among localities do remain.

Table 2.6 - Hierarchical analysis of genetic variation excluding samples from the White and Twisp Rivers

	Among major tribs (F_{TP})	Among spawning areas, within major tribs (F_{ST})	Among broodyears, within spawning areas (F_{YS})
point estimate	-0.000802	0.002045	0.005823
95% confidence interval	0.002326 -0.003669	0.003817 0.000540	0.009292 0.002453

Fitting population genetic models to the patterns of variation

In order to gain greater insight into what types of population structure could produce the observed patterns of genetic variation among localities, we fitted two types of population models to the genetic data. One model assumes that no gene flow occurs among the groups and that the genetic differences among the groups are due to random genetic drift that has occurred since the groups split from a common ancestral population. The other model assumes that the groups are in equilibrium between gene flow and genetic drift. Each model and its associated assumption will be discussed below. It is important to understand that neither of these models is likely to exactly describe the population structure of Upper Columbia spring chinook. These models may still be useful, however, because they allow rough estimates to be made of what types of population structure scenarios are or are not consistent with the observed patterns of genetic variation.

Isolation model -

The first model we fit to the data was a two population, complete isolation model. This model assumes that two populations have diverged from a common ancestral population t generations ago and have not had any gene flow between them since that time. Additional assumptions include discrete generations, random mating within populations, and complete neutrality of sampled genetic variation. Violation of the discrete generations assumption (as will occur with most Pacific salmonid species) is not expected to substantially affect the outcome of the model over the course of several generations or longer (Waples 1990). Under this model, the expected relationship between F_{ST} and divergence time in generations, t , is $t/2N_e \approx -\ln(1 - F_{ST})$ (Weir 1996, p. 194), where N_e is the harmonic mean of the effective size of each population. Estimates of $t/2N_e$ for each pair of sampled locations are shown in the lower diagonal of Table 2.7.

Island migration model -

The second model we fit was an n -deme island migration model (Slatkin 1991; Wright 1978). This model assumes that there are n randomly mating demes that all exchange migrants equally, so that every generation a fraction m of each deme consists of migrants drawn randomly from all the other demes. Additional assumptions include discrete generations, complete neutrality of the genetic variation surveyed, and equilibrium between gene flow and genetic drift. Under this model, the expected relationship between F_{ST} and the migration parameter, m , is $F_{ST} \approx 1/(4N_e m a + 1)$, where $a = (n/(n - 1))^2$ (Slatkin 1991). Using this relationship, and assuming that n is sufficiently large that $a \gg 1$, we estimated the average effective number of migrants per generation, $N_e m$, among sampling areas to be 15 - 34 if the White and Twisp River samples are included, and 65 - 462 if the White and Twisp River samples are excluded. These could be biased upwards if the actual number of demes is small. In order to further understand how samples from specific locations contribute to these average values, we estimated of F_{ST} and Nm between all pairs of sampling locations under the assumption that $n = 2$ (Table 2. 7 above the diagonal). Although these are likely to be at best extremely imperfect estimates of actual gene flow among these locations, the relative magnitudes of these estimates do suggest which populations could be more connected by gene flow than others. In examining this table, however, it is critical to understand that some key assumptions underlying this model are almost certainly violated in the case of Upper Columbia spring chinook. In particular, if populations were largely homogenized by the GCFMP project approximately 11.5 salmon generations ago, estimates of gene flow could be biased substantially upwards for some populations. For example, mark/recapture data (discussed in section 2.6 below) suggest that straying between the Chiwawa and Chewuch River has been very low, yet the estimates of Nm in Table 2.7 would suggest that gene flow between these groups has been relatively high. A possible explanation for this discrepancy is that 11.5 generations have not been sufficient for these two demes to come to equilibrium between gene flow and genetic drift.

Table 2.7 - Pairwise estimates of Nm (above diagonal), estimates of $t/2N_e$ (below diagonal)

	Chiwawa	Nason	White	Methow	Twisp	Chewuch
Chiwawa	95% confidence interval	29.73	1.94	9.93	2.03	16.88
		Very high	12.16	41.63	12.69	Very high
Nason	0.0080		2.13	Very high	2.25	5.56
	0.0000		15.84	Very high	24.32	Very high
White	0.0308	0.0385		1.79	0.95	1.45
	0.0080	0.0159		8.39	3.48	8.83
Methow	0.0104	0.0109	0.0426		2.36	5.37
	0.0000	0.0018	0.0101		15.17	231.42
Twisp	0.0289	0.0368	0.0664	0.0282		2.92
	0.0081	0.0182	0.0260	0.0120		23.97
Chewuch	0.0074	0.0200	0.0459	0.0140	0.0263	
	0.0000	0.0057	0.0137	0.0053	0.0063	

¹ Values labeled "Very high" indicate that the F_{ST} estimate was negative and there was therefore no evidence of genetic differentiation among the samples. Values of $t/2N_e$ equal to 0 indicate no significant differentiation among those pairs of sampling localities.

Estimating effective population size

The estimates of t/N_e or $N_e m$ would be easier to interpret if estimates of the effective size, N_e were available, so that t and m could be estimated separately from N_e . We used temporal differences in allele frequencies among broodyears and the level of non-independence of allele frequencies among loci to obtain two nearly independent estimates of the effective number of *breeders* (N_b) in each sampling locality for which sufficient data existed to make these estimates (Tables 2.8 and 2.9- methods reviewed by Waples 1991). The temporal method requires information about the average age structure of spawners. For the 1,269 individuals used in this study, the average age structure was: 4% age three, 58% age four, and 38% age five (values similar to the age structure reported by Chapman et al. (1995)). A very small number of six-year-old fish were included in with the five year-olds. This estimate of age structure may be somewhat biased because larger, older fish are more likely to be sampled than smaller, younger fish. We used this average age structure for all of the estimates in Table 2.8. We used Tajima's (1992) method of estimating the expected number of generations between samples. In order to better satisfy the temporal method's assumption of a closed population, known hatchery strays were excluded from these analyses, with the exception of Chiwawa hatchery fish in the Chiwawa River and Methow Hatchery fish in the Methow River (since these are supplementation programs, we consider these hatchery fish to be effectively part of the same population as the natural spawners in these areas).

Table 2.8 - Estimates of N_b using the temporal method

Group	Brood years	Nb	lower 0.025%	upper 0.975%	Ne (=Nb X 4.3)	Harmonic mean, sampled years ¹	Harmonic mean, pre-1980	Harmonic mean, 1980-1995	Nb/N
White	85,88	155	108	210	667	184	151	31	0.84
Methow	88,89,92	78	61	97	335	318	314	140	0.25
Chewuch	88,89,92	57	44	71	245	324	268	46	0.18
Chiwawa	84,85,88, 89	115	95	138	495	945	983	250	0.12
Twisp	88,92	40	27	55	172	267	581	82	0.15
Lost							146	61	
Nason							861	128	
L. Wen							160	86	
U. Wen							45	21	

¹ Abundance data from Appendix A.Table 2.9 - Estimates of N_b using the disequilibria method

Sample	Loci	Mean sample size	r^2	Est. Nb	95% CI	
CE88	8	75.9	0.0510	8.8	4.2	17.5
CE89	11	25.8	0.0409	151.6	14.4	∞
CE92	9	36.3	0.0776	6.6	3.2	14.0
CI84	12	26.8	0.0394	161.2	16.8	∞
CI85	10	32.0	0.0612	11.1	5.1	30.8
CI88	8	64.4	0.0134	-155.9	37.2	∞
CI89	10	24.5	0.0417	372.1	13.1	∞
ME88	12	33.5	0.0262	-90.8	40.8	∞
ME89	10	45.7	0.0288	48.5	14.1	∞
ME92	9	37.3	0.0412	23.1	7.8	773.3
NA88	9	29.9	0.0345	295.4	13.4	∞
TW88	7	64.4	0.0281	26.4	7.9	295.7
TW92	10	28.1	0.0779	7.8	3.8	18.5
WH85	9	31.0	0.0351	115.6	12.3	∞
WH88	10	27.0	0.0460	37.1	9.3	∞

The estimates of N_b obtained from changes in allele frequencies over time had considerably smaller confidence intervals than the estimates from linkage disequilibrium, so we used the temporal-method estimates for the rest of our analyses. Waples (1990) showed for that for Pacific salmon $N_e \approx g N_b$, where g is the average age at reproduction. The average age of the spawners used in these analyses was 4.3 years, resulting in estimates of N_e shown in Table 2.8. We then used the harmonic means of each pair of estimates to generate the estimates of t and m in Table 2.10.

Table 2.10 - Pairwise estimates of proportion migrants (m) above diagonal *or* time since divergence (t , in generations) below diagonal

	Chiwawa	White	Methow	Twisp	Chewuch
Chiwawa	95% confidence interval	0.01	0.10	0.03	0.21
		0.09	0.42	0.20	very large ¹
White	35.0		0.02	0.01	0.02
	9.1		0.08	0.05	0.10
Methow	8.3	38.0		0.04	0.08
	0.0	9.1		0.27	very large ¹
Twisp	14.8	36.3	12.8		0.06
	4.1	14.2	5.5		0.47
Chewuch	4.9	32.9	7.9	10.6	
	0.0	9.8	3.0	2.6	

¹ estimate is greater than 1.0.

Estimated divergence time between the major tributaries as a whole

We can also use the estimate of F_{TP} (Table 2.5), to obtain estimates of either divergence time or gene flow between the Wenatchee and Methow Basins as a whole. These are $t/2N_e = 0.00186$ (95% CI = -0.00265 – 0.00628), and $Nm = 60$ (95% CI = 38 – infinity; assuming $n = 3$). One important result from these analyses is that the level of genetic differentiation among the major tributaries is at least roughly consistent with what might be expected if spring chinook salmon groups in the major tributaries were genetically homogenized during the GCFMP and have diverged independently since then. The GCFMP ended in 1943, or about 11.5 spring chinook salmon generations since the early 1990's when the bulk of the sampling used in our analyses occurred. If we use the relationship $t/2N_e = -\ln(1 - F_{TP})$ to ask what would the effective sizes in the major tributaries need to be in order to explain the observed point estimate of F_{TP} under a model of complete independence between major tributaries, we obtain a value of $N_e = 3061$. The harmonic mean abundance of the Methow River population from 1960 to 1990 was estimated to be 1012, and the harmonic mean abundance for the Wenatchee River population from 1958 to 1990 was estimated to be 2110 (data from Appendix A). Multiplying each of these estimates by the average generation time (4.3 years), results in per generation sizes of 4351 and 5881 for the Methow and Wenatchee River populations, respectively. Taking the harmonic mean of these two estimates results in a final average estimate of 5881 spawners per generation. The N_e/N ratio obtained using these estimate of N and the a value of N_e of 3061 is 0.52. This is within the range of values observed for the individual spawning areas (Table 2.8), and is also similar to the estimate Waples et al. (1993) obtained for several spawning groups of spring chinook salmon in the Snake River, suggesting that an model of isolated divergence for 11.5 generations is plausible.

3.3.2 Steelhead genetic data

Chapman et al. (1994) summarized the available steelhead allozyme data from the Upper Columbia River area as well as other selected locations. Sampling locations in the Upper Columbia area included the Chewuch, Early Winter, Methow, Mad, Entiat, Wenatchee, Mission, Icicle and Chiwawa Rivers and Wells Hatchery (Chapman et al. 1994). The main conclusions from Chapman et al.'s genetic analysis were 1)

there is no evidence of substantial genetic introgression due to releases of hatchery steelhead of non-Upper Columbia River origin, 2) there are significant allele frequency differences among all the samples, and 3) there is little or no geographic structure to the pattern of variation within the Upper Columbia River area. In other words, although there are significant differences between all sampling localities, there is no evidence of population structure at a larger spatial scale within the Upper Columbia River area. The presence of significant allele frequency differences among localities does not appear to be consistent with the large proportion of common-origin hatchery-produced fish spawning in these areas, and Chapman et al. (1994) hypothesize that the existence of natural populations of resident *O. mykiss* may explain this apparent discrepancy. In other words, the patterns of variation may reflect the existence of locally indigenous resident populations with varying levels of admixture from the steelhead hatcheries. This admixture could either be in the form of actual genetic introgression of hatchery steelhead into local resident populations, or could simply result from a mixture of sampled groups that have remained distinct.

The existence of significant allele frequency differences among samples from different areas may suggest that fish spawning in the different sampling areas could be reproductively isolated, but these data must be interpreted with some caution. In particular, the hypotheses that are actually being tested must be clearly understood. For example, Chapman et al. (1994) used chi-square contingency tests to test for significant differences in allele frequencies among samples of wild steelhead juveniles collected in 1986. The null hypothesis that is tested with this approach is that each sample is randomly drawn without replacement from a single infinite population or with replacement from a single finite population. Waples (1998) discusses several ways in which this hypothesis is routinely violated. For example, most samples are drawn from a finite population without replacement, and it is rare that every individual in the group of interest has an equal probability of being sampled. The first violation (finite populations) is 'conservative', in that it tends to reduce the power to detect differentiation, but the latter violation (non-random sampling) can result in a statistical rejection of the null hypothesis even if the samples were drawn from a single randomly mating population (Waples 1998). The data summarized by Chapman et al. (1994) are based on samples that may be non-random in at least two ways. First, all of the Upper Columbia River samples consisted of juveniles. A hypothesis of interest is that adults return and spawn at random among the sampled areas, and the use of juvenile samples can result in the false rejection of this hypothesis because differences among locations will be amplified by a generation of drift (Allendorf and Phelps 1981). Waples (1998) discussed a method of accounting for this, which we will use below. Second, steelhead in the Upper Columbia River area exhibit a large array of life-history strategies, which result in populations with overlapping age classes. This means that at any given time, it is in practice very difficult to obtain a truly random sample from a single generation of the population because not all of the members of that generation are available for sampling. The Chapman et al. (1994) are also based on juvenile samples, which may include resident *O. mykiss*. The demographic relationship between anadromous and resident *O. mykiss* is not well understood, further complicating interpretation of the genetic data. The only good way to deal effectively with the issue of potentially non-random sampling is to fully understand the biology of the organism being studied and to use this information to obtain samples as randomly as possible (Waples 1998).

With these issues in mind, we reanalyzed the data summarized by Chapman et al. (1994). Our strategy in this analysis was to calculate Wright's F_{ST} statistic to summarize the amount of variation among samples, and then to evaluate the relative probabilities that different scenarios of interest could produce that level of differentiation. We estimated F_{ST} from the data in Chapman et al.'s (1994) Table 2 using the method of Weir and Cockerham (Weir 1996). Only allele frequency data were available, so we assumed that the genotype frequencies were at Hardy-Weinberg equilibrium within populations. We obtained 95% confidence intervals for our estimates by bootstrapping over loci (1000 replicates, Weir 1996). Only 10 loci were used in these analyses, and not all populations were scored for all loci, so these confidence intervals are only approximate. The estimates are presented in Table 2.11.

Table 3-11 - Estimates of F_{ST} for Upper Columbia River steelhead

F _{ST}	All wild samples from 1985 ¹	1984 and 1985 Wenatchee R. samples ²	1983 and 1985 Entiat R. samples ³	1983 and 1985 Methow R. samples ⁴
estimate	0.0307	0.0140	0.0197	0.0074
95%	0.0141	-0.0004	0.0046	-0.0073
confidence interval	0.0541	0.0344	0.0340	0.0340

¹ Samples 1, 2, 3, 4, 6, 7, 8, 10, and 14 from Chapman et al. (1994, Table 2). 1985 refers to the broodyears; fish were collected in 1986 (Hershberger and Dole 1987). ² Samples 14 and 15. ³ Samples 4 and 5. ⁴ Samples 8 and 9.

When all wild samples from 1985 are considered together, the 95% percent confidence interval for F_{ST} does not include zero, indicating that we can reject the hypothesis that all the samples were drawn randomly with replacement from the same group of fish (Table 2.11). This result is equivalent to the observation of statistically significant allele frequencies differences among these samples (Chapman et al. 1994) discussed above, and suffers from the same difficulties of interpretation. The last three columns in Table 2.11 provide estimates of the variability between samples collected at different times in the same locations. The large number of age classes expressed by Upper Columbia River steelhead combined with the fairly short duration between sampling times (one or two years) means that these temporal samples can roughly be considered samples from the same generation. They therefore provide a rough upper bound of the contribution of non-random sampling and drift between adults and juvenile progeny to the estimate of F_{ST} among 1985 samples from different locations. If the average of these three temporal F_{ST} estimates is subtracted from the 1985 geographic estimate, this results in 95% confidence interval of 0.0004 to 0.04.

Unfortunately (for our purposes), a large number of historical scenarios could produce a value of F_{ST} within this range. For example, groups isolated for t generations will have an expected value of F_{ST} equal to approximately $1 - e^{-t/2N}$ (Weir 1996). An estimate of F_{ST} in the range 0.0004 - 0.04, therefore, is consistent with a single generation of drift among populations of effective size 12.5 to 1250. In 1985, about 12,000 and 8000 steelhead returned to spawn in the Methow/Okanogan and Wenatchee/Entiat Rivers, respectively. Assuming an Ne/N ratio of about 0.3 (based on Waples et al. 1993 estimates for spring chinook), this translates into about 3600 and 2400 effective breeders, respectively. We do not know how these breeders distributed themselves among the areas sampled, but 12.5 to 1250 effective breeders per sampling area does not seem unreasonable. This means that it is possible that a single generation of drift could have led to the observed level of divergence among the 1985 samples. The genetic data therefore do not rule out the possibility that samples were drawn from a single independent population as defined above.

On the other hand, if instead of assuming complete isolation among sampling areas we assume that the sampling areas conform to an equilibrium 'island' model of migration where all populations exchange migrants equally and are at equilibrium between migration and drift, we can use the estimate of F_{ST} to estimate the number of migrants exchanged per generation (Nm , Weir 1996, p. 183). Under the island model, a rough estimate of Nm can be obtained from the relationship $F_{ST} = 1 / (4Nm + 1)$. Using this relationship, estimates of Nm consistent with an estimate of F_{ST} in the range of 0.0004 to 0.04 range from about 5 to 600. These are estimates of the genetically effective number of migrants, and the actual number of individuals moving from one spawning area to another could be considerably higher. Even so, the lower end of this range is probably not consistent with the sampling areas all being part of the same independent population, while the upper end of the range could well be consistent with a single population.

In summary, we agree with the conclusions of Chapman et al. (1994): that the limited genetic data available provide no evidence of substantial population structure within the Upper Columbia River area, but neither do these data completely rule out the existence of such structure.

3.4 Life-history data or morphological data

3.4.1 Spring chinook salmon

Data on length, sex and age was available for each of the individuals used in the genetic analyses of spring chinook salmon (section 2.3.1). We compared the length at age for fish from the same broodyear but sampled from different spawning locations, and found several statistically significant differences among localities (nested ANOVA; Table 2.12). For example, four year old males from the White River were significantly larger than four year old males from Nason Creek for the 1985 and 1988 (but not 1989) broodyears. These differences could be due to a variety of factors, including genetic drift between isolated groups, natural selection, or phenotypic plasticity, or random environmental effects.

Table 2.12 - Differences in length-at-age among spawning localities

Brood Year	Sex	Age	Pops Included	P-value of differences within basin	P-value of differences among basins	Direction of departure
1985	Male	4	CI, NA, WH	0.000	N/A	WH > CI, NA
1985	Female	4	CI, NA, WH	0.315	N/A	
1987	Female	4	CI, WH	0.08	N/A	
1988	Male	4	CE, TW, NA, WH	0.034	0.000	Wen > Meth WH > NA (?) CE > TW
1988	Female	4	CE, TW, CI, NA, WH	0.003	0.113	WH > CI, NA TW > CE (?)
1988	Male	5	CI, NA	0.003	N/A	CI > NA
1989	Male	4	CE, TW, CI, NA, WH	0.196	0.210	
1989	Female	4	CE, TW, ME	Non sig	N/A	Needs rerun
1992	Male	4	CE, TW, ME	0.212	N/A	

3.5 Environmental and habitat variation

There are several notable environmental features which differ among the spawning areas. Although these differences by themselves do not provide information on the demographic connectedness of different spawning groups, they do suggest the possibility that groups in different streams could experience natural selection for local adaptations, which may be important to consider in evaluating the likelihood of reproductive isolation among groups.

Water Quality

Water quality within the subbasins, influenced by geology, vegetation, and continuity with submerged aquifers, among other factors, differs among basins (Figures 2.7, 2.8).

Gradient

Gradient profiles between the primary spawning grounds of the main tributaries are quite different (Figure 2.9). The Mad River in the Entiat Basin has the highest mean gradient, while the White River in the Wenatchee Basin the lowest.

Temperature

Temperatures differ in the several tributaries, both during summer spawning periods (Figure 2.10) and in terms of total annual temperature units Figure (2.11).

Geomorphology

Another notable difference between streams is the presence or absence of a lake or lake system. The Entiat and Methow have no lake systems within the anadromous zone, while the Wenatchee and Okanogan are affected substantially by their lake systems. The White River is far more glacially influenced than other spawning streams in the area (Mullan et al. 1992). The rivers also differ in characteristics such the ratio of pools to riffles (Figure 2.12)

Figure 2.7 - Conductivity of spawning streams (data from Mullan et al. 1992)

Comparison of the Mean Conductivity of the Principal Spawning Streams in the Upper Columbia

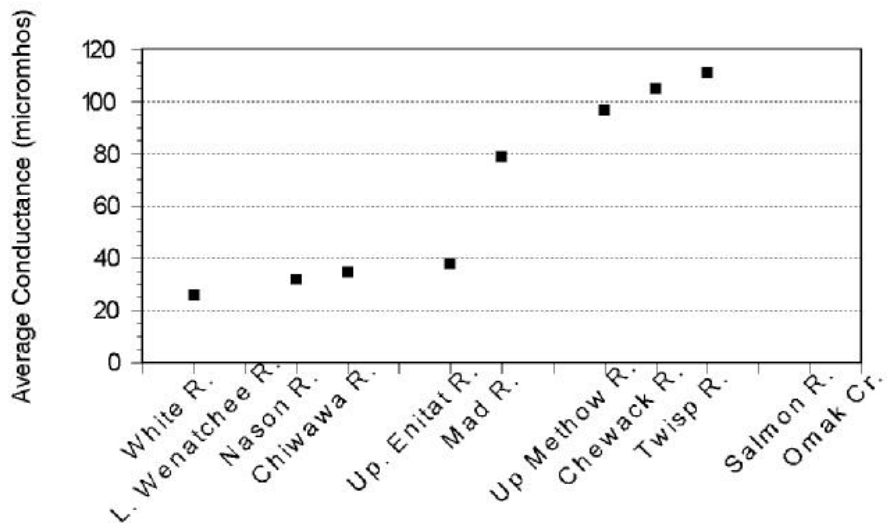


Figure 2.8 - Total dissolved solids in Upper Columbia River streams (data from Mullan et al. 1992)

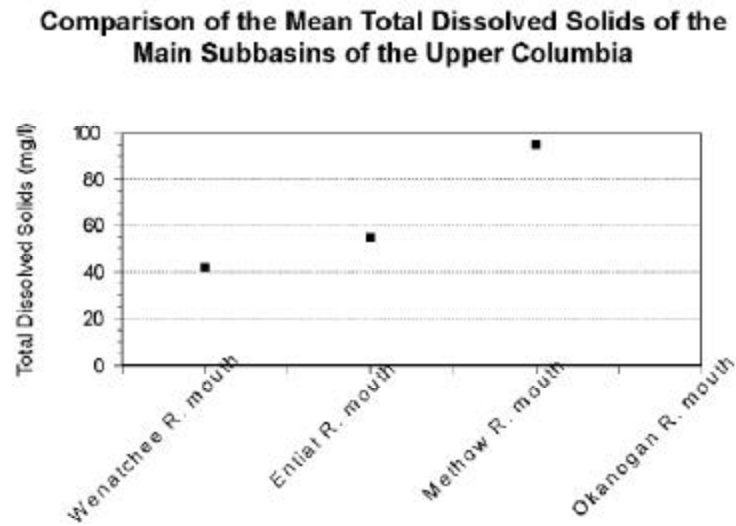


Figure 2.9 - Gradient of Upper Columbia River spawning streams (data from Mullan et al. 1992)

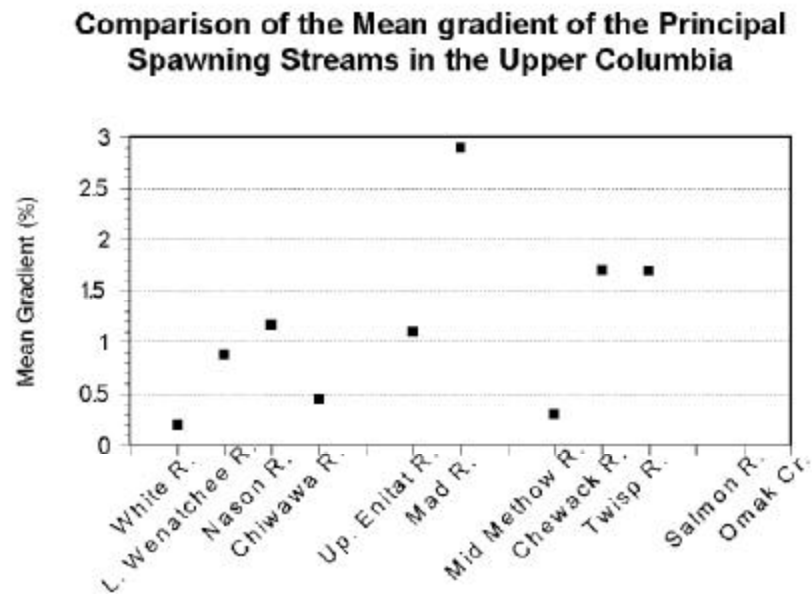


Figure 2.10 - Temperature of spawning streams in the Upper Columbia River area (data from Mullan et al. 1992)

Comparison of the Mean July-September Temperatures of the Main Subbasins of the Upper Columbia

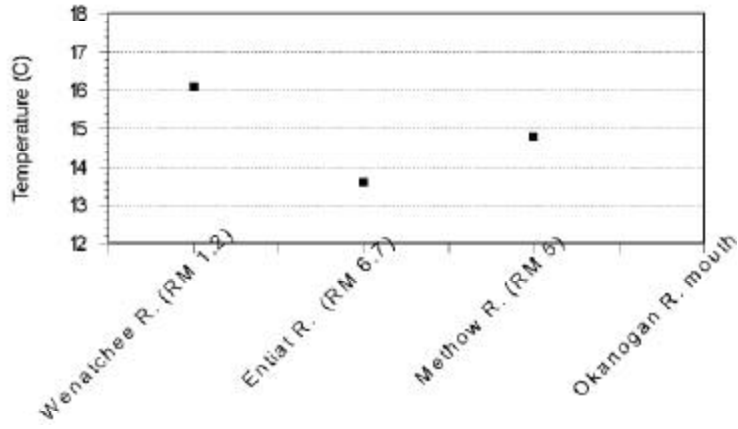


Figure 2.11 - Annual temperature units for Upper Columbia spawning streams (data from Mullan et al. 1992)

Comparison of the Annual Temperature Units of the Principal Spawning Streams in the Upper Columbia

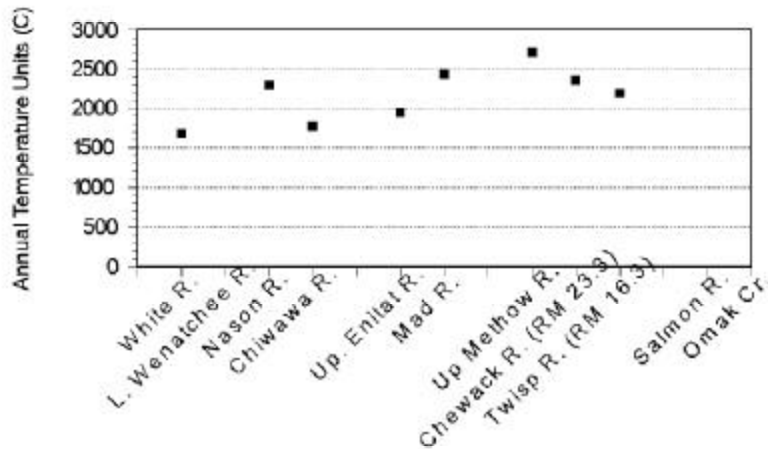
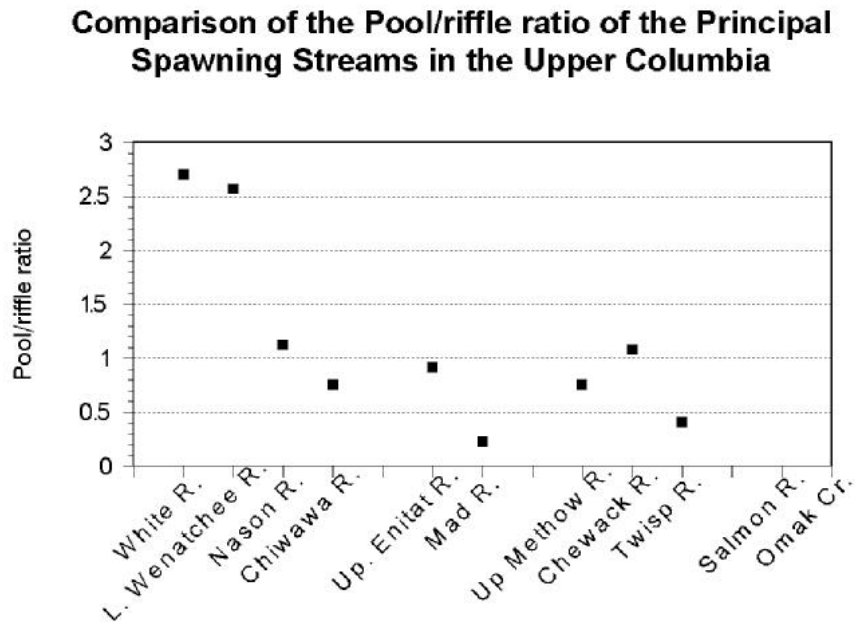


Figure 2.12 - Pool/riffle ratios for Upper Columbia River spawning streams (data from Mullan et al. 1992).



3.6 Straying data

3.6.1 Spring chinook salmon straying data

Marking juvenile fish in their "home" area and then observing the rate at which they return to this or other areas is one method of directly estimating the rate of exchange among putative populations (e.g. Labelle 1992). No studies of this type exist for wild Upper Columbia spring chinook salmon, but a portion of the spring chinook salmon raised in hatcheries and released in the tributaries in the area are marked or tagged as juveniles. The locations at which these marked hatchery produced fish return can be used to gain insight into possible patterns of straying of natural-origin fish.

Straying of spring chinook released in the Chiwawa river: There has been a spring chinook salmon supplementation project on the Chiwawa River since 1989. Because this project uses broodstock captured in the Chiwawa River, the patterns of straying exhibited by marked Chiwawa supplementation fish might be expected to reflect patterns of straying of natural origin Chiwawa spring chinook salmon. Spring chinook juveniles are transferred from the Eastbank facility to the Chiwawa rearing and acclimation ponds in September. The fish are reared through the winter on Chiwawa River water (or Wenatchee River water if freezing conditions preclude the use of Chiwawa water), and then are volitionally released in April of the following year (Chapman et al. 1995). All of the hatchery produced spring chinook released in the Chiwawa River are marked and/or tagged. Table 2.13 shows the reported recovery locations (Upper Columbia area only) of hatchery spring chinook released in the Chiwawa River (data obtained from Susan Markey, WDFW). Only four tagged fish released in the Chiwawa River were recovered in Upper Columbia River areas outside of the Wenatchee River Basin (excluding Eastbank Hatchery), compared to 169 recoveries within the Wenatchee River Basin and 19 recoveries at Eastbank Hatchery. Within the Wenatchee River Basin, 37 tags were recovered in the Chiwawa River or Chiwawa Hatchery, 40 in Nason Creek, 15 in the Upper Wenatchee, 1 in the White River, and 4 in Icicle Creek (Table 2.13). In 1997 spring chinook were collected for broodstock at Tumwater Dam, and 70 tags were recovered at this location. Within Wenatchee River Basin, the proportion of sampled fish with Chiwawa Hatchery tags was highest in samples from the Chiwawa River and Nason Creek (up to 100% in the Chiwawa River and 33% in Nason Creek), and lowest in White River, Little Wenatchee River and Icicle Creek (5%, 0% and 2%, respectively; Table 2.14).

Table 2.13 - Recovery locations of tagged hatchery spring chinook released in the Chiwawa River

tag code	recovery year	recovery location	obs	est
635327	1997	CHIKAMIN CR 45.0798	1	0
631156	1994	CHIWAHA HATCHERY	1	1
634014	1994	CHIWAHA HATCHERY	1	1
631156	1992	CHIWAHA R 45.0759	2	0
631156	1993	CHIWAHA R 45.0759	5	30
631156	1994	CHIWAHA R 45.0759	2	26
634646	1995	CHIWAHA R 45.0759	2	10
634748	1996	CHIWAHA R 45.0759	1	2
635326	1996	CHIWAHA R 45.0759	2	5
635326	1997	CHIWAHA R 45.0759	1	0
635326	1998	CHIWAHA R 45.0759	3	0
635327	1996	CHIWAHA R 45.0759	4	10
635327	1997	CHIWAHA R 45.0759	4	0
635327	1998	CHIWAHA R 45.0759	3	0
635352	1998	CHIWAHA R 45.0759	1	0
635952	1995	CHIWAHA R 45.0759	4	19
635326	1997	CHIWAHA+TUMWATER FCF	40	40
635327	1997	CHIWAHA+TUMWATER FCF	30	30
635352	1997	CHIWAHA+TUMWATER FCF	1	1
631156	1991	COLUMBIA R AT PRIEST	1	0
635326	1998	EASTBANK HATCHERY	5	0
635327	1998	EASTBANK HATCHERY	1	0
635352	1998	EASTBANK HATCHERY	13	0
634014	1993	HANFORD REACH (36)	1	18
631156	1993	ICICLE CR 45.0474	1	5
635327	1997	ICICLE CR 45.0474	3	0
631156	1994	LEAVENWORTH HATCHERY	1	1
631156	1993	NASON CR 45.0888	15	61
634748	1996	NASON CR 45.0888	1	24
635326	1997	NASON CR 45.0888	7	0
635327	1997	NASON CR 45.0888	12	0
635352	1998	NASON CR 45.0888	2	0
635327	1997	ROCK CR 45.0842	3	0
635952	1995	WELLS DAM SP CHANNEL	1	1
635327	1997	WELLS W LADDER TRAP	1	1
631156	1993	WENATCHEE R 45.0030	4	11
631156	1993	WENATCHEE R 45.0030	9	34
634646	1995	WENATCHEE R 45.0030	1	1
635952	1995	WENATCHEE R 45.0030	1	1
631156	1993	WHITE R 45.1116	1	7

Table 2.14 - Estimated proportion of Chiwawa Hatchery fish among natural spawners in Upper Columbia River spawning streams (data from Susan Markey, WDFW)

Recovery year	Recovery location	Number of natural spawners sampled	Chiwawa H. tags recovered	tags/sample size	tag codes
1993	CHIWAWA R 45.0759	40	5	0.125	631156
1994	CHIWAWA R 45.0759	14	2	0.142857	631156
1995	CHIWAWA R 45.0759	6	6	1	634646 635952
1996	CHIWAWA R 45.0759	23	7	0.304348	634748 635326 635327
1993	ENTIAT R 46.0042	10	0	0	
1994	ENTIAT R 46.0042	5	0	0	
1993	ICICLE CR 45.0474	46	1	0.021739	631156
1994	ICICLE CR 45.0474	9	0	0	
1993	LTL WENATCHEE 450985	19	0	0	
1994	LTL WENATCHEE 450985	1	0	0	
1993	METHOW R 48.0002	107	0	0	
1994	METHOW R 48.0002	48	0	0	
1996	METHOW R 48.0002	90	0	0	
1993	NASON CR 45.0888	123	15	0.121951	631156
1994	NASON CR 45.0888	14	0	0	
1995	NASON CR 45.0888	3	0	0	
1996	NASON CR 45.0888	3	1	0.333333	634748
1993	PESHASTIN CR 45.0232	1	0	0	
1993	WENATCHEE R 45.0030	51	9	0.254902	631156
1994	WENATCHEE R 45.0030	4	0	0	
1995	WENATCHEE R 45.0030	2	2	1	635952
1993	WHITE R 45.1116	20	1	0.05	631156
1994	WHITE R 45.1116	1	0	0	

Straying of fish released Methow River - Table 2.15 shows the recovery locations of tagged spring chinook released from Methow Hatchery (data from Susan Markey, WDFW). Only one tagged Methow Hatchery fish has been recovered in the Entiat River, and no tagged Methow Hatchery fish have been recovered in the Wenatchee River Basin. Within the Methow, patterns of straying are difficult to describe because in 1996 and 1998 all spring chinook were collected at Wells dam. In 1997, Methow Hatchery tags were recovered from spawners in the Methow, Twisp, Chewuch and Entiat Rivers.

Table 2.15 - Recovery locations of spring chinook released from Methow Hatchery

tag code	recovery year	recovery location	obs	est
634127	1997	CHEWUCH R 48.0728	6	0
635161	1997	CHEWUCH R 48.0728	2	0
635329	1997	CHEWUCH R 48.0728	1	0
635551	1997	ENTIAT R 46.0042	1	0
635329	1997	HANFORD REACH (36)	1	0
635551	1997	HANFORD REACH (36)	1	0
634127	1998	METHOW HATCHERY	12	0

634515	1998 METHOW HATCHERY	1	0
634848	1995 METHOW HATCHERY	1	1
635161	1998 METHOW HATCHERY	2	0
635329	1998 METHOW HATCHERY	3	0
635350	1998 METHOW HATCHERY	1	0
635410	1998 METHOW HATCHERY	2	0
635416	1998 METHOW HATCHERY	2	0
635417	1998 METHOW HATCHERY	1	0
635418	1998 METHOW HATCHERY	2	0
635419	1998 METHOW HATCHERY	2	0
635551	1998 METHOW HATCHERY	24	0
636037	1998 METHOW HATCHERY	4	0
636038	1998 METHOW HATCHERY	1	0
636039	1998 METHOW HATCHERY	2	0
636040	1998 METHOW HATCHERY	1	0
634127	1997 METHOW R 48.0002	3	0
635410	1997 METHOW R 48.0002	1	0
635551	1997 METHOW R 48.0002	5	0
635329	1997 TWISP R 48.0374	1	0
635410	1998 WELLS HATCHERY	1	0
634127	1996 WELLS W LADDER TRAP	32	32
634127	1997 WELLS W LADDER TRAP	36	36
634331	1996 WELLS W LADDER TRAP	6	6
634332	1996 WELLS W LADDER TRAP	2	2
634848	1996 WELLS W LADDER TRAP	6	6
634849	1996 WELLS W LADDER TRAP	4	4
634850	1996 WELLS W LADDER TRAP	16	16
634851	1996 WELLS W LADDER TRAP	10	10
635121	1996 WELLS W LADDER TRAP	4	4
635122	1996 WELLS W LADDER TRAP	4	4
635123	1996 WELLS W LADDER TRAP	8	8
635124	1996 WELLS W LADDER TRAP	14	14
635125	1996 WELLS W LADDER TRAP	2	2
635133	1996 WELLS W LADDER TRAP	2	2
635135	1996 WELLS W LADDER TRAP	6	6
635136	1996 WELLS W LADDER TRAP	10	10
635137	1996 WELLS W LADDER TRAP	2	2
635138	1996 WELLS W LADDER TRAP	6	6
635139	1996 WELLS W LADDER TRAP	8	8
635140	1996 WELLS W LADDER TRAP	4	4
635141	1996 WELLS W LADDER TRAP	4	4
635161	1997 WELLS W LADDER TRAP	9	9
635329	1996 WELLS W LADDER TRAP	10	10
635329	1997 WELLS W LADDER TRAP	6	6
635350	1997 WELLS W LADDER TRAP	2	2
635410	1997 WELLS W LADDER TRAP	13	13
635551	1996 WELLS W LADDER TRAP	8	8
635551	1997 WELLS W LADDER TRAP	83	84
635609	1996 WELLS W LADDER TRAP	2	2
635609	1997 WELLS W LADDER TRAP	1	1
634127	1997 WINTHROP NFH	16	16
635161	1997 WINTHROP NFH	1	1

635329	1997 WINTHROP NFH	3	3
635350	1997 WINTHROP NFH	2	2
635410	1997 WINTHROP NFH	2	2
635551	1997 WINTHROP NFH	41	41

Recoveries of marked fish from other hatchery programs: Chapman et al. (1995), reviewed the patterns of CWT recoveries of spring chinook released in Icicle Creek by the Leavenworth NFH, and concluded that very few of these fish return to areas other than Icicle Creek. Tables listing all of the coded wire tags recovered from within the Wenatchee, Entiat and Methow River Basins are reported in Appendix C.

Summary of straying data: The information available suggests that the rate of straying of hatchery spring chinook among the major tributaries is very low. Within Wenatchee River Basin, in several years significant numbers of Chiwawa River hatchery fish strayed to other areas in the Wenatchee Basin, with the bulk of the recoveries occurring in Nason Creek and the Upper Wenatchee River.

3.7 Summary of previous conclusions regarding population structure

3.7.1 Spring chinook salmon

WDF et al. (1993) recognized nine stocks of wild spring chinook salmon in the Upper Columbia River area, spawning in the Chiwawa, Nason, Little Wenatchee, White, Entiat, Methow, Twisp, Lost, and Chewuch Rivers. The stocks were identified primarily on the basis of geographic location, and (in some cases) statistically significant differences in allele frequencies from other stocks. The stock definition WDF et al. (1993) used in making this determination was not identical to our definition of an independent population.

3.7.2 Steelhead

WDF et al. (1993) concluded that the steelhead spawning in the Wenatchee, Entiat, and Methow/Okanogan River, were each part of a separate 'stock'. This conclusion was based on the geographic isolation of the spawning populations. The stock definition WDF et al. (1993) used in making this determination was not identical to our definition of an independent population.

3.8 Discussion and conclusions regarding population structure:

3.8.1 Spring chinook salmon population structure

As a group, we discussed a variety of hypotheses about Upper Columbia River spring chinook salmon population structure, including scenarios with as few as a single independent population and as many as eleven or more independent populations. Based on the data and analyses discussed above, we suggest that historically there were probably at least three independent populations of spring chinook salmon in the Upper Columbia River area. These spawned in the Wenatchee, Entiat and Methow River Basins. There is some anecdotal evidence that the Okanogan River Basin may have also contained an independent spring chinook salmon population. There are two primary lines of evidence supporting a three or four independent population hypothesis: 1) The spring chinook spawning grounds in these four major tributaries are geographically isolated from each other by lower reaches of the tributaries and sections of the mainstem Columbia River (Figures 2.1 and 2.2). Chinook salmon are generally not expected to stray at substantial rates between rivers of this size (reviewed by Quinn et al. (1991)); 2) Mark/recapture studies with hatchery reared spring chinook released in the Upper Columbia River area provide direct evidence that rates of straying among the major tributaries are low (section 2.6). Other evidence supporting this conclusion includes: 1) Trends in redd counts are somewhat less correlated among the major tributaries than within the major tributaries (Figure 2.5); 2) There are significant differences in length-at-age between

fish sampled from the different major tributaries (Table 2.12); and 3) The major tributaries differ with respect to several environmental variables, which could promote reproductive isolation (section 2.5). The low level of genetic divergence observed between spawners in the major tributaries is consistent with this scenario if populations were substantially homogenized during the GCFMP (section 2.3.1).

There is still some uncertainty about whether or not there are (or were) multiple independent populations within one or more of these major tributaries. Some particular areas of uncertainty are discussed below:

White River/Little Wenatchee River - We concluded that there is uncertainty about whether spawners in the White River (possibly combined with the Little Wenatchee due to its geographic proximity) should be considered an independent population in their own right or a subpopulation of a greater Wenatchee River population. The evidence pointing toward demographic independence is: 1) The White River samples are the most distinctive in terms of allozyme allele frequencies, and based on these frequencies the estimated rate of gene flow from other areas is quite low (section 2.3); 2) Very few marked Chiwawa Hatchery fish have been recovered in the White River (section 2.6); and 3) Lake Wenatchee may geographically separate the spawning grounds in the White and Little Wenatchee Rivers from other areas in the Wenatchee River Basin (section 2.1)

The evidence pointing toward non-independence is: 1) During the GCFMP (1939-1943) adult spring chinook trapped at Rock Island Dam were planted only in Nason Creek or were artificially spawned. Planted adults in Nason Creek were fenced in to keep them from spawning elsewhere, and artificially propagated fish were not released in the White River or any other tributaries other than Nason Creek (Chapman et al. 1995). Assuming that these actions had the effect of eliminating spawning in the White River for at least several years, this implies that the current White River (sub)population resulted from recolonization soon after the GCFMP ended. This suggests that the spawners in the White River are effectively demographically connected to other spawning groups, because if the White River spawners were to go extinct they could be rapidly recolonized by fish from other areas; 2) The estimated spawning abundance in the White and Little Wenatchee Rivers has never been particularly large, and has always been far lower than simple population viability guidelines of several thousand spawners per year (see section 3.1.2 below). An estimate of the potential spawning abundance in the White River based on habitat area also suggests that this (sub)population does not have the potential to be very large (D. Chapman, pers. com.). Together, these data suggest the possibility that even if it is independent, the White River population might not have a negligible risk of extinction over a 100 year time frame; 3) Even prior to the GCFMP, spring chinook spawning abundance in the Upper Wenatchee River Basin was very low (Fish and Hanavan 1948; Mullan et al. 1992), further suggesting that current patterns of population structure in Wenatchee River are of relatively recent origin. The level of genetic differentiation between the White River sample and other samples is consistent with the hypothesis that the White River (sub)population diverged from the other groups after 1943 (Table 2.10)

Icicle Creek - We concluded that the spawners in Icicle Creek are probably currently part of an independent population that also includes spawners in Leavenworth NFH. This conclusion is supported by mark/recapture data (section 2.6 and Appendix C) and the lack of abundance correlations with any other index area (Figure 2.5). However, this independence may be due to the strong influence of Leavenworth NFH. The historical degree of isolation between spring chinook spawning in Icicle Creek and other spawning groups in the Wenatchee River Basin is not known, although the mark/recapture data suggest that Chiwawa River spring chinook do not stray in large numbers to Icicle Creek. The Icicle Creek spawning area may be geographically separated from other areas in the Wenatchee River Basin by Tumwater Canyon (Figure 2.1), but we do not know if this potential geographic isolation would result in substantial reproductive isolation from other areas in the Wenatchee River Basin over 100 year time frames. In any case, the stock currently being propagated at the Leavenworth NFH is not considered to be part of the Upper Columbia spring chinook ESU, so the current Icicle Creek population cannot be 'counted' for recovery purposes (NMFS 1999).

Twisp River - Samples from the Twisp River are nearly as genetically distinctive as those from the White River at the allozyme loci surveyed, and the estimates of divergence time and gene flow suggest that spawners in the Twisp River could be substantially reproductively isolated from other groups (section 2.3).

On the other hand, the spawning areas in the Twisp River are not geographically disjunct from other spawning areas in the Methow River Basin, and mark/recapture experiments suggest that homing fidelity of hatchery fish released in the Twisp River is not particularly high (Table 2.14 and Appendix C). During the GCFMP, neither adults nor juveniles were released into the Twisp River (Chapman et al. 1995), suggesting that the current (sub)population there may be the result of recolonization shortly after the GCFMP ended. If so, this suggests that recolonization would occur quickly following extinction, suggesting a demographic connection to other spawning groups in the basin.

Summary and conclusions for spring chinook salmon - We believe that the weight of the evidence suggests that there are (or historically were) three or four independent populations of spring chinook salmon in the upper Columbia River Basin, inhabiting the Wenatchee, Entiat, Methow, and (possibly) Okanogan River basins. There appears to be considerable population substructure within one or more of these major tributaries (see, e.g., discussion on the White and Twisp Rivers above), however, and this population substructure should be considered when evaluating recovery goals and management actions. Spring chinook spawning in Icicle Creek and Leavenworth NFH are an independent population, but this population is not considered part of the Upper Columbia spring chinook ESU (NMFS 1999).

3.8.2 Steelhead population structure

A complete understanding of the historical population structure of Upper Columbia steelhead appears impossible to achieve. However, based primarily on current and historical spawning distributions and the assumption of reasonably accurate homing rates, we believe that historically there were at least three (possibly four) major populations of steelhead in the Upper Columbia River area, one each in the Wenatchee, Entiat, Methow and (possibly) Okanogan River Basins. Due to lack of detailed data on spawning locations and straying patterns, the very limited nature of the existing genetic data, and long history of extensive artificial propagation of Upper Columbia River steelhead, it is impossible rule out the possibility that one of more of these major tributaries could have historically contained more than one independent population.

Since the late 1960's (and perhaps since the 1940's), steelhead in the Upper Columbia River area may have been functionally part of the same population, due to very large scale supplementation from a common hatchery subpopulation. The existing genetic data are consistent with this conclusion, but they do not rule out the possibility that independent populations have persisted despite large scale supplementation (section 2.3.2). Even if large scale supplementation has resulted in a single independent population, this does not preclude multiple independent populations from existing in a recovered ESU (see discussion in section 4.1).

4 Spring chinook salmon: Interim recovery goals

The recovery goals discussed below are intended to be used for the purposes of jeopardy analyses until an Upper Columbia River recovery team sets final recovery criteria. The interim recovery goals discussed below may therefore be revised or modified by the recovery team.

4.1 Number of populations

Current status: Currently, we believe there are three independent populations in the Upper Columbia spring chinook salmon ESU, spawning in the Wenatchee, Entiat and Methow River Basins.

Interim recovery level: We suggest that a reasonable interim recovery level is at least three independent, viable populations, one each in the Wenatchee, Entiat and Methow River basins. The Okanogan River has apparently not supported a spring chinook population since at least the 1930's, so we see little point in setting interim recovery goals for this potential population at this time. Rather, we suggest deferring discussion of goals for the spring chinook in the Okanogan River basin to an Upper Columbia River recovery team.

Having at least three populations will reduce the probability that a single catastrophic event could cause the extinction of the entire ESU. Multiple populations within an ESU will also increase the likelihood that a diversity of phenotypic and genotypic characteristics will be maintained. This will allow for the operation of natural evolutionary processes important for the long-term persistence of the ESU.

4.2 Population abundance

We pursued several strategies for obtaining interim recovery abundance levels. First, we reviewed the historical record to determine the abundance of the populations during times when they were considered to be relatively healthy. Accurate abundance estimates for Upper Columbia salmonid populations are only available for approximately the last 50 years, although Mullan et al. (1992) attempted to roughly estimate salmonid abundance in the Upper Columbia prior to large-scale European immigration. Second, we attempted to estimate the current carrying capacity of the Upper Columbia tributaries, and compared these to estimates of what the capacity might have been historically. Third, we used results from population modeling to determine population abundance levels that would result in a low risk of extinction. For the current document we used very general modeling results drawn from the conservation biology literature. We expect more detailed, population-specific modeling to occur at a later time.

We also pursued several strategies for obtaining lower abundance thresholds that indicate varying levels of risk to the populations. These lower thresholds were obtained both from past observations of Upper Columbia salmonid abundance, as well as general modeling results drawn from the published conservation biology literature. These lower thresholds and their biological meaning will be discussed further below.

The stated purposes of the ESA are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, to provide a program for the conservation of such endangered species and threatened species, and to take such steps as may be appropriate to achieve these purposes (ESA sec. 2(b)). The ESA's focus is, therefore, on natural populations and the ecosystems upon which they depend. Artificial propagation of a listed salmonid species is therefore not a substitute for eliminating the factors causing or contributing to a species' decline (Hard et al. 1992). In order to satisfy these objectives of the ESA, all of the abundance criteria discussed below apply to natural-origin spawners, which are defined as the progeny of fish that spawned in the wild.

Historical spawning abundance

Beamesderfer et al. (1997) used redd count data to estimate the annual spawning abundance of spring chinook populations in the Upper Columbia River area (Appendix A). Based on these data, Figures 3.1-3.3 show the annual estimated spawning abundance and running 8-year geometric mean abundance for the Wenatchee, Entiat and Methow River populations. Until the early 1970's, the harvest rate on spring chinook in the mainstem Columbia River ranged from 25% to 64% (Beamesderfer et al. 1997), so the potential spawning escapements during that time period ranged from ~130% to ~280% of the actual escapements.

Figure 3.1 - Wenatchee River spring chinook salmon spawning abundance (data from Beamesdurfer et al. 1991)

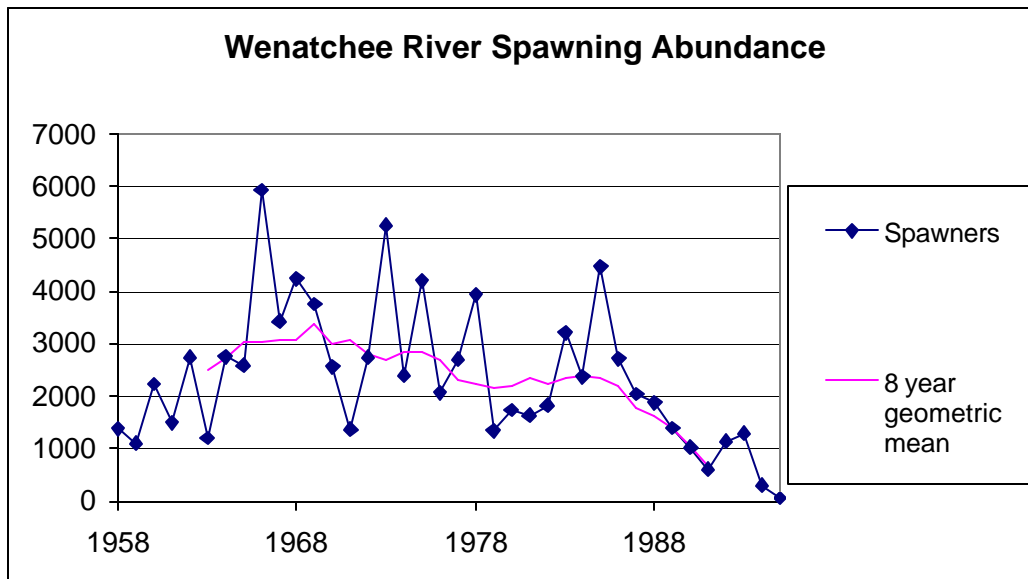


Figure 3.2 - Entiat River spring chinook salmon spawning abundance (data from Beamesdurfer et al. 1991)

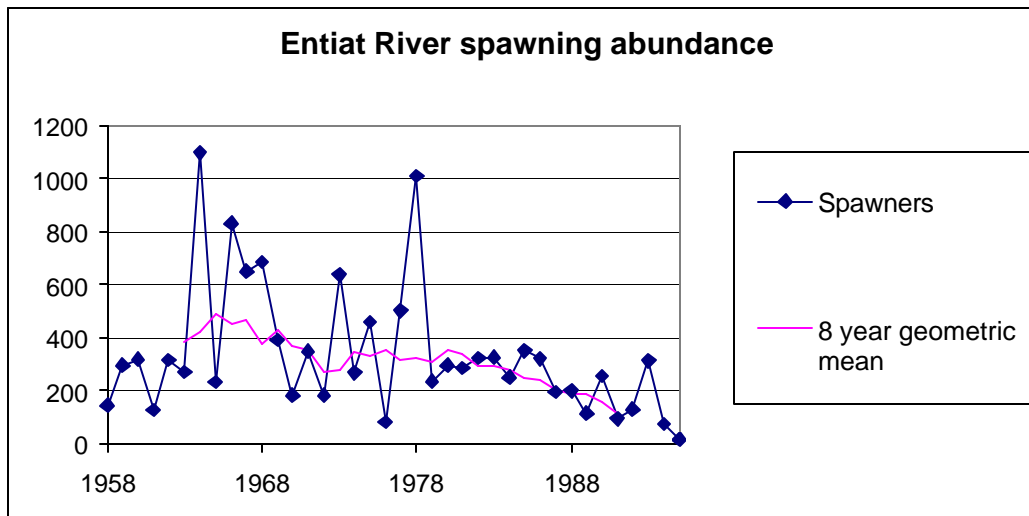
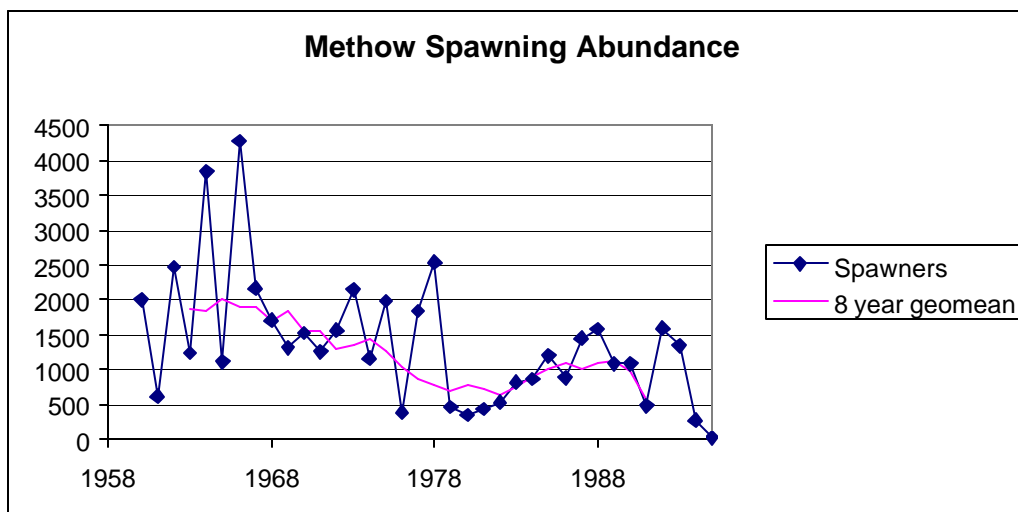


Figure 3.3 - Methow River spring chinook salmon spawning abundance (data from Beamesdurfer et al. 1991)



Current spawning/rearing habitat capacity:

We compared several methods for estimating the carrying capacity of the Upper Columbia tributaries (Table 3.1).

Table 3.1 - Estimates of habitat capacity for spring chinook salmon

	Wenatchee	Entiat	Methow
Smolt Capacity¹			
Chapman estimates based on effective drainage area (221 smolts/sq. mi.)	312052	65195	375921
Chapman estimates corrected for Mullan HQI accuracy (.84)	262144	54764	315774
Adult equivalents for Chapman estimates based on 1.3% smolt-adult survival.	3408-4057	712-848	4105-4887
Adult equivalents for Chapman estimates based on 4% egg-smolt survival, 4100 eggs/female and 1:1 sex ratio	3197-3806	668-795	3851-4584
Parr Density²			
Fisher estimates (19.17/100m ²)	1060101	122688	835812
Smolt equivalents for Fisher estimates (14.7-40% overwinter survival)	155835-424040	18035-49075	122864-334325
Adult equivalents for Fisher estimates (1.3% smolt-adult survival)	2026-5512	234-638	1597-4346
Adult equivalents for Fisher estimates based on 4% egg-smolt survival, 4100 eggs/female and 1:1 sex ratio	1900-5171	220-598	1498-4077
Mullan-Chapman estimates (basin-specific densities)	1045170	64000	436000
Smolt equivalents for Mullan-Chapman estimates (14.7-40% overwinter survival)	153640-418068	9408-25600	64092-174400
Adult equivalents for Mullan-Chapman estimates (1.3% smolt-adult survival)	1997-5434	122-333	833-2267
Adult equivalents for Mullan-Chapman estimates based on 4% egg-smolt survival, 4100 eggs/female and 1:1 sex ratio	1874-5098	115-312	782-2127
Schaller et al. (1999) estimates³	4808	496	1379

Notes:

¹ Don Chapman suggested an approach based on effective drainage area, defined as the area upstream from the lower limit of rearing by stream annulus salmon and steelhead, basically the area above water where the daily maxima reaches 22°C. Chapman calculates the Wenatchee, Entiat and Methow basins have 1412, 295, and 1701 mi² of effective drainage, respectively. He then calculated the yield of smolts per square mile of effective drainage for the Snake basin during the mid-60's, a period considered to be full seeding, arriving at 222 spring chinook smolts/mi². The correction of 0.84 results from a comparison of a similar analysis of steelhead smolts, which resulted in 81 smolts/mi², for a total of 275965 smolts for the three basins combined. Chapman assumed that the habitat quality index (HQI) total of Mullan et al. (1992) (Appendix H, Table 8) of 231898 was more accurate. The HQI total was 84% of the effective drainage total. Chapman assumed that the same correction could be applied to spring chinook smolt capacities based on effective drainage area. The value of 1.3% smolt-adult survival is a mean of values in Mullan et al. (1992). The values of 4% egg to smolt survival and 4100 eggs/female came from Chiwawa River monitoring data (Tracy Hillman, personal communication).

² Parr density- Tim Fisher and Don Chapman both suggested approaches based on parr densities. Fisher used a value of 19.17 parr/100m², an average from IDFG Snake basin habitat monitoring reports for 1984-1995, and applied this value to all three basins. Fisher also used an overwinter survival value of 14.7%, a mean from Snake River streams (Paulsen and Fisher 1999). The Mullan-Chapman values came from Chapman's summary of density data in Mullan et al. (1992), and thus were basin specific: 18.9 parr/100m² for the Wenatchee, and 10.0 parr/100m² for the other two basins. All calculations above assumed the same rearing areas:

Wenatchee: 553 ha; Entiat: 64 ha; and Methow: 436 ha. These values were from Mullan et al. (1992). The tabulated ranges reflect the application of the two overwinter survival rates to both Fisher and Mullan-Chapman estimates. The smolt-adult survival value used was the same as for the smolt capacity estimates.

³ Schaller et al. (1999) fitted spawner-recruit data from 1958-1995 (Wenatchee), 1955-1995 (Entiat) and 1960-1995 (Methow) to a Ricker production model in the form $R = e^{aSe^{bS}}$. The values in Table 3.1 are the number of spawners that would produce maximum recruitment, and are estimated as $1/b$ (Hilborn and Walters 1992) where the b values are from Table 2 of Schaller (1999).

Potential spawning/rearing habitat capacity with habitat improvements

Due to time constraints, we were unable to quantify the degree to which habitat improvements might be expected to increase the capacity or productivity of the Upper Columbia River tributaries. NMFS et al. (1998), discuss extensive habitat problems in the Wenatchee, Entiat, Methow and Okanogan watersheds, and make numerous conservation and restoration recommendations. Some of the analyses conducted by the Columbia River Basin system planning process also suggest that habitat capacity could be substantially increased through restoration actions (WDF 1990). In its proposed rule to list several Pacific salmon ESUs, the NMFS cited local habitat problems in the Upper Columbia River area (FR Vol. 63 pp. 11482-11520).

Extinction modeling

We expect that population viability modeling will be performed as part of the Upper Columbia River QAR process. We have not performed such detailed modeling at this time, however. Instead, we summarize some more general results in order to determine if the ranges of adult spawning population sizes obtained from habitat capacity estimates and historical escapement data appear to be in the range needed to produce a low risk of extinction.

Demographic guidelines: Under the assumption that population size is log-normally distributed, Thomas (1990) used observed levels of population size variability to recommend 'safe' (i.e. low risk) population sizes for a variety of classes of organisms. For vertebrate species with high levels of year-to-year variation in population size (such as Pacific salmon), Thomas suggested that a population size of ~10,000 or more per generation would be reasonable to produce a low risk of extinction. For salmon species with multiple age classes, ~10,000 or more spawners per generation would translate into several thousand or more spawners per year, assuming that spawners/year = (spawners/generation)*(generations/year). For example, if Upper Columbia spring chinook salmon have a generation time of ~4.3 years, then ~10,000 spawners/generation would be equal to ~2300 spawners per year.

Genetic guidelines - In a recent review, Lynch (1996) suggested that an effective population size of ~1000/generation will be adequate for a population to have a low risk of extinction from loss of genetic variability or accumulation of deleterious mutations. Lande (1995.) suggested that an effective size of ~5000/generation was necessary. For Pacific salmon, the effective population size per generation is approximately equal to the effective number of breeders per year multiplied by mean age at reproduction (Waples 1990). Based on the results in section 3.3 and those of Waples et al. (1993.), 0.3 may be a reasonable estimate of the typical ratio of effective number of breeders to actual number of breeders for spring chinook salmon. Assuming that Upper Columbia spring chinook salmon have a mean age of reproduction of 4.3 years and an effective to actual breeder ratio of 0.3, an effective size of 1000 to 5000 per generation translates into a geometric mean annual spawning abundance of about 775 - 3875 ($N_e/(4.3 * 0.3)$).

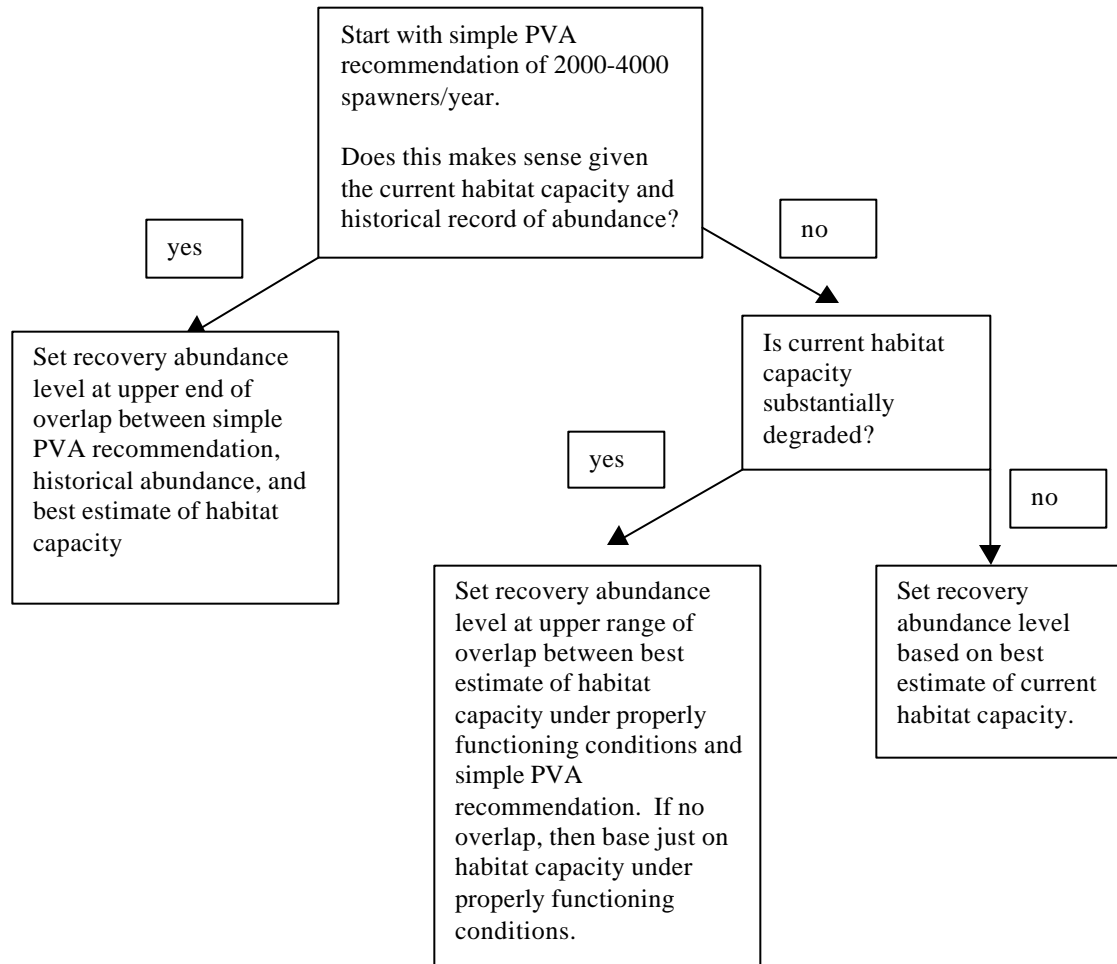
Interim recovery criteria:

In setting interim recovery abundance levels, we used the following train of logic (Figure 3.4): Start the process with a simple PVA recommendation of 2000-4000 spawners per year, based on a combination of the demographic and genetic recommendations from the conservation literature discussed in the preceding section. If this range overlaps with the range of values obtained from estimates of current habitat capacity (Table 3.1) and historical abundance (Figure 3.1-3.3) then choose a value near the upper end of the overlap among these ranges. If the range of values from the simple PVA recommendation is substantially higher than the estimates of current habitat capacity and/or historical abundance, then determine if current habitat

capacity is substantially degraded. If current habitat capacity is not substantially degraded, then base recovery abundance levels on the current habitat capacity. If current habitat capacity is substantially degraded from historical or pristine conditions, then set the recovery abundance level near the upper end of the overlap between the simple PVA recommendations and the habitat capacity expected under recovered habitat conditions, or just the recovered habitat capacity if this is lower than the simple PVA recommendations. If the range of values from the simple PVA recommendations is substantially lower than current or future carrying capacity estimates, then set the interim recovery levels at or above the simple PVA recommendations and above the population size where compensatory effects are expected to be important in that population.

In our process for setting interim recovery abundance levels, we recommend that when the abundance ranges suggested by general PVA results, habitat capacity and historical abundance overlap, the upper end of the range of overlap be used as the interim recovery level. The rationale for choosing a value at the upper end of the range of overlap is that there is considerable uncertainty associated with both the estimates of habitat capacity and the simple PVA recommendations. In the face of such uncertainty, we have chosen to use the upper end of the range of overlap in order to err on the side of being conservative (i.e. lower risk of extinction) in setting interim recovery abundance levels. If population modeling demonstrates that the recovery levels determined in the above manner are either overly conservative or result in a higher than acceptable risk of extinction, then the recovery levels should be reevaluated.

Figure 3.4 - Flow chart of logic train for setting interim recovery abundance levels



Based on this approach, we discuss interim recovery abundance levels for each population below:

Wenatchee River population: We recommend an interim recovery abundance level for the Wenatchee River population of 3750 naturally produced spawners/year, a value that falls within the range of the habitat capacity estimates, historical run sizes, and simple PVA recommendations.

Entiat River population: We recommend an interim recovery abundance level for the Entiat River population of 500 naturally produced spawners/year. This value does not fall within the range of the simple PVA recommendations, but is consistent with the estimated current and historical habitat capacity and historical run sizes. In this report, we have not attempted to quantify the capacity of the Entiat River watershed under improved habitat conditions. NMFS et al. (1990) describe numerous potential habitat improvement strategies that for the Entiat River watershed, so the final recovery goals for the Entiat River spring chinook population may be larger than the interim goal recommended here.

Methow River population: We recommend an interim recovery abundance level for the Methow River population of 2000 naturally produced spawners/year, a value that falls within the range of the habitat capacity estimates, historical run sizes, and simple PVA recommendations.

Incorporating uncertainty into the interim recovery abundance levels

In setting the abundance and return rate thresholds for recovery or delisting purposes, it is important to incorporate uncertainty about population status (Botsford and Brittnacher 1998). There are two general types of uncertainty that have to be taken into account. First, populations change size from year to year from random environmental and demographic factors. It is important that this variation be incorporated into delisted criteria so that a population's status will not be misjudged on just a few good (or bad) years. Second, in many cases there will be uncertainty associated with the annual estimates of population size themselves. This uncertainty could cause a population's status to be seriously misjudged if the actual population size is substantially different from the estimated size. Because of both types of uncertainty, it is important that a population's 'status' with regard to recovery goals be judged using multiple years of data.

We used the variance in past abundance estimates as way of exploring how taking into account uncertainty affects the interim recovery abundance levels. By assuming that future abundance will be log-normally distributed with variance equal to the estimated variance of past abundance estimates, it is possible to determine how many years of observation might be necessary to be statistically confident that the observed geometric mean abundance is greater than the interim recovery abundance level (Appendix D). We believe that is the role of policy makers to decide how certain they want to be that interim recovery levels have been achieved, and in Table 3.2 we provide several examples of the relationship between the observed geometric mean abundance, the number of years of observation, and the statistical confidence that the geometric mean abundance is greater than the interim recovery level. Note that the values in Table 3.2 are based on an assumption that methods of estimating abundance will remain the same as the methods used to generate the estimates made by Beamesderfer et al. (1997). If in the future the methods for estimating abundance change, these analyses will need to be reevaluated.

Table 3.2 - Observed geometric mean abundance necessary to be confident that the actual mean is above the interim recovery threshold

population		Observed geometric mean		
confidence level		years of observation over which geometric mean is estimated		
	interim recovery threshold	8	12	16
Methow	2000			
95%		2943	2741	2627
85%		2550	2438	2374
75%		2342	2274	2235
65%		2187	2151	2130
55%		2058	2047	2040
Entiat	500			
95%		732	683	655
85%		636	608	592
75%		584	568	558
65%		546	537	532
55%		514	512	510
Wenatchee	3750			
95%		6215	5665	5360
85%		5156	4863	4696
75%		4613	4441	4341
65%		4221	4130	4077
55%		3897	3870	3853

Lower abundance levels:

As a committee, we believed that it would be useful to identify several abundance levels below the interim recovery levels that indicate varying levels of risk to the population. Assessing the relative likelihood of exceeding these levels may be useful in deciding among alternative management actions. These abundance levels and their biological significance are discussed below and summarized in Table 3.3.

Table 3.3 - Summary of lower abundance levels

Level	Biological meaning
Absolute extinction level. Equal to one or fewer spawners for five or more consecutive years.	The independent population is completely extinct. Use of an absolute extinction criterion in population models that do not incorporate Allee effects may result in overly optimistic estimates of persistence time.
Quasi-extinction level. Equal to 50 or fewer spawners per year (Methow and Wenatchee) or 30 or fewer spawners per year (Entiat) for five or more consecutive years.	Abundance level at which a population is believed to 1) be at extremely high risk of extinction in the immediate future, and 2) faces risks that are not usually incorporated into simple population extinction models.
Cautionary level. 1200 spawners/year in the Wenatchee River 150 spawner/year in the Entiat River 750 spawners/year in the Methow River	Abundance level below which historically the population would be expected to fall only about 10% of the time. Escapements consistently below these levels indicate increasing risk and uncertainty about population status.

Absolute extinction level: We define an independent population as extinct when it contains 1 or fewer spawners per year for 5 or more consecutive years. The time span of five years is based on the observation that only a very small percentage of Upper Columbia spring chinook return to spawn at ages greater than five years (Chapman et al. 1995 and section 3.3 of this report).

Quasi-extinction level: Many simple extinction models do not take into account potential compensatory effects that may occur at very low abundance levels. For example, the variance of population size might be expected to increase at low abundance levels due to demographic stochasticity. Very small populations may also be significantly affected by demographic or genetic effects that are rarely incorporated into PVA models, such as mate-finding ability or inbreeding depression. For these reasons, PVA analyses often make use of quasi-extinction levels, which are abundance levels higher than absolute extinction but at which the risk of extinction is believed to be very high (Ginzburg et al. 1982). The primary reason we are setting quasi-extinction levels is to aid in the population viability analyses of the Upper Columbia River populations. These levels do not necessarily correspond to threshold levels for any particular management action.

Quasi-extinction levels that have been used in the past for salmon populations typically fall in the range of 50-200 individuals. For example, Botsford and Brittnacher (1998) used 100 female spawners a year as a quasi-extinction threshold for winter-run chinook salmon, and did not include compensation in their viability model. Their rationale for this level was based on evidence for compensation at about 100 females for two salmon populations (Myers et al. 1995), and on the very large (>100,000) historical winter-run chinook salmon population size. Nickelson and Lawson (1998) in their extinction analysis of Oregon coastal coho salmon used 50 spawners per year as a quasi-extinction threshold in addition to including several compensatory factors in their model. In a population viability analysis of Snake River spring/summer chinook salmon, Emlen (1995) did not use a quasi-extinction threshold or include compensation in his model. Similarly, Ratner et al. (1997) did not include compensation or a quasi-extinction threshold in their

population viability analysis of Umpqua River spring chinook salmon. Allendorf et al. (1997.), in a very general discussion of salmonid population viability, suggested a population with 250 spawners *per generation* was at very high risk of extinction. Assuming ~4.3 years per generation, 250 spawners per generation would be equivalent to about 60 spawners per year for Upper Columbia spring chinook salmon. In their unpublished extinction analysis of individual Snake River spring/summer chinook populations, the NWFSC's Cumulative Risk Initiative group has used one spawner in one year as a quasi-extinction threshold (P. Kareiva, personal communication).

For purposes of this report, we recommend that a spawning population size of 30 spawners or less per year for 5 or more consecutive years as a reasonable quasi-extinction threshold for Entiat River population, and 50 spawners per year for 5 or more consecutive years as a reasonable quasi-extinction threshold for the Wenatchee and Methow River populations. These values are based on the professional opinions of the members of the biological requirements workgroup and recommendations from the conservation biology literature (e.g., Ginzburg 1982; Dennis et al. 1991; and references in preceding paragraph). The Entiat River quasi-extinction threshold is lower than the other two because the Entiat River Basin is substantially smaller than either the Wenatchee or Methow River Basins and the Entiat River population has always been considerably smaller than either the Wenatchee or Methow River populations.

Cautionary level: The committee decided that it would be useful to identify an abundance level below which demographic, genetic, and other risk factors to the populations become of increasing concern, and uncertainties in production response become magnified. These levels (one for each population) were determined primarily from the lower end of the spawning abundances exhibited by the Upper Columbia populations during the time period when they were considered to be relatively healthy (Table 3.4; see Appendix E for details).

Table 3.4 - Cautionary abundance levels for Upper Columbia spring chinook populations

Basin	Cautionary level (total spawners)
Wenatchee R.	1200
Entiat R.	150
Methow R.	750

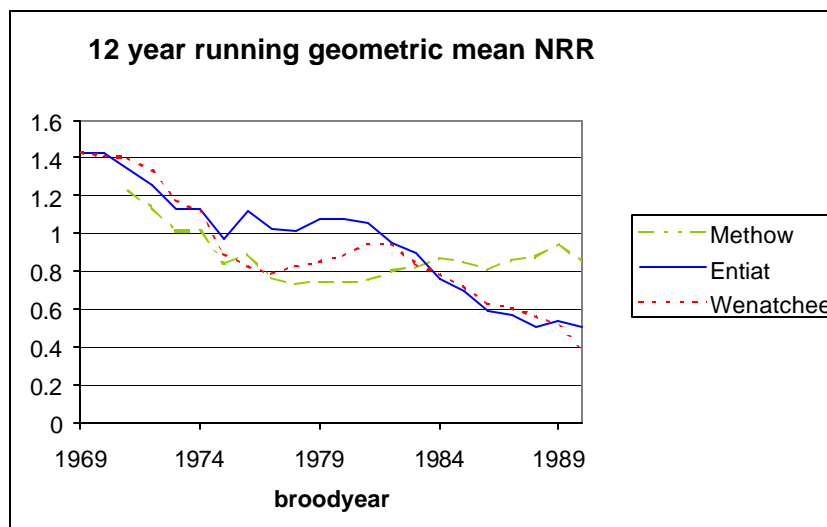
4.3 Population growth rate

The purpose of having a population growth rate recovery parameter is to ensure that a population is naturally self-sustaining and not dependent upon artificial propagation for its persistence. The natural return ratio (NRR) is a useful statistic for this purpose (Busby et al. 1994.). The NRR is calculated as the number of natural origin spawners originating from a particular broodyear divided by the number of natural spawners (regardless of origin) in that broodyear. If there are no naturally spawning hatchery fish, then the NRR is simply a spawner:spawner ratio, and a stable population will have a geometric mean NRR of 1.0. If there are significant numbers of naturally spawning hatchery fish, then the NRR is an index of the degree to which the population is naturally self-sustaining, under the assumption that naturally spawning hatchery fish have the same reproductive success as natural-origin fish. A growing population, or a population with an increasing proportion of natural origin spawners, will have an NRR greater than 1.0.

Current status:

The twelve-year running geometric mean NRR's for Wenatchee, Entiat and Methow populations are plotted in Figure 3.5 for the broodyears running from 1958 to 1995. The estimated 12-year geometric mean NRR of the spring chinook populations in the Upper Columbia River area has not been greater than 1.0 since the mid-1970's (Wenatchee River and Methow River populations) or mid-1980's (Entiat River population).

Figure 3.5 – Twelve-year running geometric mean natural return rates for Upper Columbia spring chinook populations. In the plot, the geometric mean is calculated from the plotted broodyear and eleven preceding broodyears. Data are from Beamesdurfer et al. (1997) ("Obsrvd (S/S)" columns of Tables G.4, H.4 and I.4.)



Interim recovery criteria: In order to be considered recovered, a population must have a geometric mean NRR significantly greater than 1.0. Table 3.5 describes the relationship between the observed geometric mean NRR needed to be confident the true mean is greater than 1.0, the number of broodyears of observations and the desired confidence level (see Appendix D for details). Note that because it takes five years for each complete brood cycle, the number of years of observation needed to obtain n broodyears is $n+5$.

In the long term, a stable population without hatchery straying is expected to have a geometric mean NRR of 1.0. This means that over the long-term, it will not be possible to have an NRR that is significantly greater than 1.0. As a recovery criteria, however, it is appropriate to require that the NRR be greater than 1.0, because all of the Upper Columbia spring chinook populations are currently much smaller than they need to be in order to be considered recovered. In order for these populations to meet their recovery abundance levels and sustain themselves naturally, the geometric mean NRR will therefore need to be greater than 1.0.

Table 3.5 - Observed geometric mean NRR necessary to be confident that the actual mean is above the interim recovery threshold

population		Observed geometric mean		
confidence level		brood years of observation over which geometric mean is estimated		
	interim recovery threshold	8	12	16
Methow	> 1.0			
95%		1.6592	1.51199	1.43052
85%		1.37582	1.29758	1.25307
75%		1.23076	1.18475	1.15814
65%		1.12594	1.10169	1.08749
55%		1.03944	1.03209	1.02773
Entiat				
95%		2.37957	2.0296	1.84597
85%		1.72677	1.56207	1.47147
75%		1.42688	1.33677	1.28578
65%		1.22517	1.18036	1.15442
55%		1.06847	1.05557	1.04795
Wenatchee				
95%		3.88813	3.03055	2.61222
85%		2.35288	2.01099	1.83131
75%		1.74514	1.57563	1.48252
65%		1.37452	1.29658	1.25224
55%		1.10931	1.0884	1.07611

4.4 Population substructure

In identifying independent populations of Upper Columbia spring chinook, we recognized that the populations we identified are not homogenous. For example, there are significant allele frequency difference among samples from different tributaries within both the Wenatchee and Methow River systems, strongly suggesting that mating does not occur randomly within these populations. The importance of this population substructure to the viability of Upper Columbia spring chinook salmon populations is not immediately clear, but there are theoretical reasons and empirical observations from other species that suggest that population substructure can play an important role in population persistence (Hanski and Gilpin 1991). For example, in the Wenatchee and Methow Rivers (and to a lesser degree the Entiat River), spring chinook salmon and steelhead are distributed in several streams with varying environmental characteristics (see section 2.5 and Mullan et al. (1992)). Distribution into multiple spawning streams may increase population persistence by avoiding limiting the population's exposure to single-stream catastrophic environmental events.

Current status:

Wenatchee River population: Currently, wild spring chinook spawn primarily in five tributaries within the Wenatchee River Basin: Nason Creek, Chiwawa River, Little Wenatchee River, White River, and the Upper Wenatchee River (Figure 2.1). Since the 1950's, the bulk of the spawning has occurred in the Chiwawa River and Nason Creek (Figure 3.6). Historically, wild spring chinook also spawned in Icicle Creek, and perhaps in other smaller tributaries below Tumwater Canyon (Mullan et al. 1992). Currently, the spring chinook spawning in Icicle Creek are primarily of Leavenworth NFH origin, and spring chinook (and all anadromous fish) are limited to the lower 2.8 miles of Icicle Creek due to the hatchery diversion

dam (Mullan et al. 1992). Several streams in the lower Wenatchee Basin, particularly Mission, Chumstick Creeks and Peshastin Creeks, are moderately to highly degraded (Mullan et al. 1992).

Methow River population: Currently spring chinook spawn throughout the Methow River Basin, but primarily in four streams (Figure 2.2): the Methow, Twisp, Chewuch and Lost Rivers. The proportion of spawners is relatively evenly divided among these areas, although there is considerable year-to-year variation (Figure 3.7).

Entiat River population: The Entiat River Basin is considerably smaller than either the Wenatchee or Methow River Basins, and contains fewer good spring chinook spawning areas (Mullan et al. 1992; Figure 2.1). Spawning primarily occurs in the Entiat River proper, and perhaps in the lower section of the Mad River (Figure 2.1; Mullan et al. (1992)).

Figure 3.6 - Proportion of redd counts in different Wenatchee River tributaries (data from Appendix A)

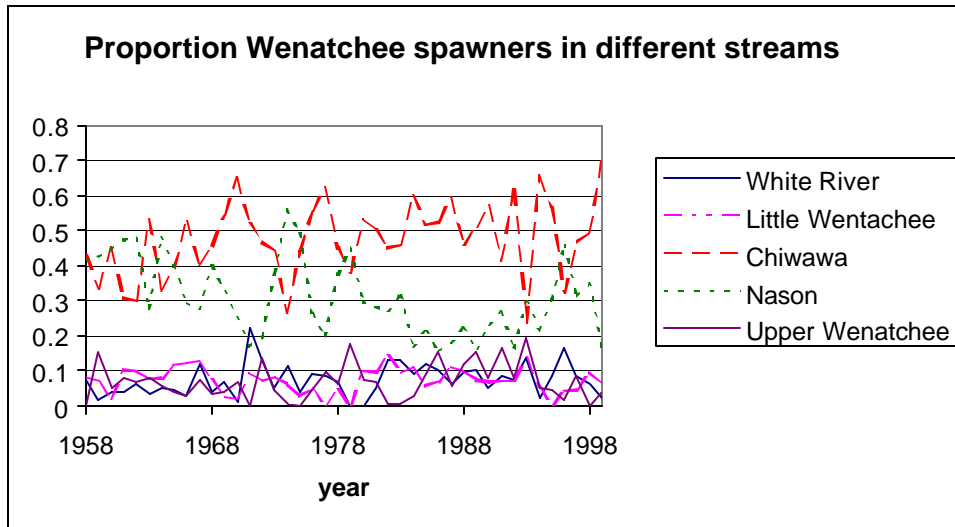
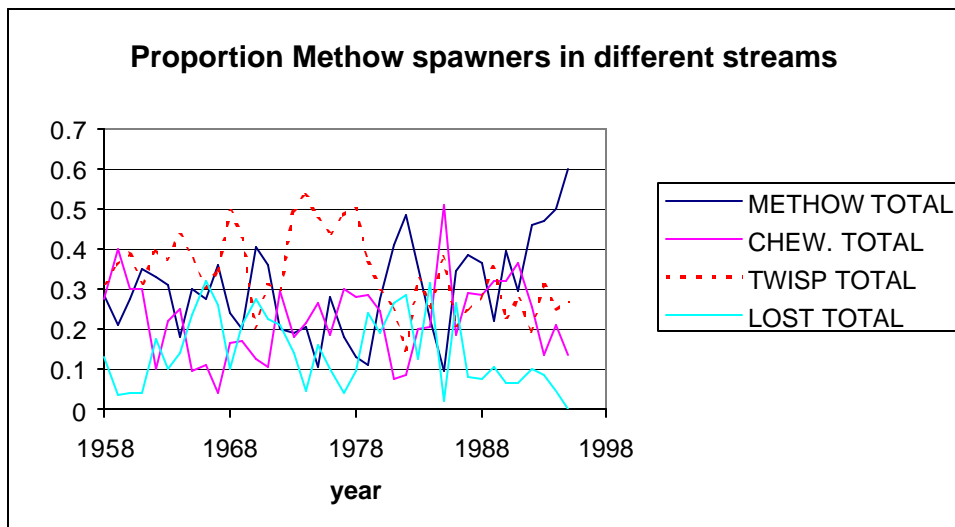


Figure 3.7 - Proportion of redd counts in different Methow River tributaries (data from Appendix A)



Interim recovery level:

Qualitative criteria that apply to all populations: In order to be considered recovered, spring chinook populations should be able to utilize properly functioning habitat in multiple spawning streams within each major tributary, with patterns of straying among these areas free from human-caused disruptions.

Quantitative criteria:

Wenatchee River population: Averaged over 12 years, Wenatchee River spring chinook should spawn in at least three streams within the Wenatchee River Basin, with each stream containing at least 5% of the total spawning abundance.

Methow River population: Averaged over 12 years, Methow River spring chinook should spawn in at least three streams within the Methow River Basin, with each stream containing at least 5% of the total spawning abundance.

Entiat River: No quantitative criteria.

Rationale: There are two reasons why we believe that it is important that recovery criteria contain a way of assessing the distributions of spawners within the Wenatchee and Methow River Basins. First, spring chinook have historically spawned in several major streams within the each of these areas (Figures 2.1 and 2.2), and these streams differ in their physical characteristics (see section 2.5 and Mullan et al. (1992). This diversity of habitats suggests the possibility that subpopulations within these basins could potentially be or become locally adapted, and these potential adaptations could be important to the fitness of the populations as a whole. The evidence of limited straying and gene flow between some spawning groups occupying different streams within the Wenatchee River Basin (see sections 2.3 and 2.6) further suggests that such local adaptations are possible. Second, we believe that populations as a whole will have a lower risk of extinction if they are distributed into several different streams because they would be less vulnerable to natural or man-made environmental catastrophes that occur in any one stream. Third, the quantitative criteria have always been met based on the historical distribution of spawners from the time series 1958-99, suggesting that this is a reasonable standard for the future. Finally, we recognize that the distribution of spawners may change naturally over time. The quantitative criteria above recognize this by requiring that spawners be distributed among streams but not requiring a specific number of spawners in any particular stream.

4.5 Diversity

In a spatially and temporally varying environment, there are two general reasons why diversity is important for species and population viability. First, diversity within a species (or ESU) provides a buffer against changes in the environment across spatial scales and over relatively short time periods. Different life history or genetic variants have different likelihoods of persisting, depending on local environmental conditions. Therefore, the more diverse a population, the more likely some individuals are to survive and reproduce in the face of environmental change. Second, genetic diversity is the raw material for the future evolutionary adaptability of a population, ESU, or species to long-term environmental changes. Salmonids regularly face changes in their freshwater, estuarine and ocean environments due to natural and human causes; thus we expect that within- and among-population diversity will be important to their persistence.

Actions that affect basic demographic and evolutionary processes (e.g., patterns of mutation, selection, drift, recombination, migration, population turnover) have the potential to alter patterns of diversity within a species. For example, the levels of straying and gene flow among populations are important factors influencing the maintenance of diversity within and among populations. Such strays may or may not successfully reproduce and leave offspring. Gene flow refers to the movement of genes from one population to another, and results from strays that successfully reproduce. There are a number of ways in

which human actions could substantially alter patterns of straying, and therefore potentially alter patterns of diversity and adaptation among salmonid populations. For example, blocking migration corridors by dams or dewatering of rivers could prevent salmonids from homing and increase the rate of straying into other populations. Artificial propagation, by transplanting populations or selecting for domestic traits, can also affect patterns of diversity.

Current status:

Spring chinook in the Upper Columbia River had declined dramatically by the 1930's, and then were substantially genetically shuffled during the GCFMP from 1939-1943 (Chapman et al. 1995; Mullan et al. 1992). From the mid-1940's until the recent severe declines in the 1990's, natural populations of spring chinook have presumably been relatively free to evolve naturally and adapt to local conditions. Over the last decade, spring chinook population have declined rapidly (Appendix A), and intensive artificial propagation management actions in response to these declines may have some affects on the patterns of diversity that evolved over the last ~60 years. For example, in 1996 and 1998 all spring chinook passing Wells dam were captured and artificially propagated for release into the Methow River and its tributaries, with unknown effects patterns of genetic diversity within the Methow River population.

Currently, spring chinook of Carson stock origin³ are released from Leavenworth, Entiat and Winthrop National Fish Hatcheries. The NFH broodstocks are not considered to be part of the same biological ESU as the wild Upper Columbia River populations (NMFS 1999), and interbreeding between the NFH stocks and the wild populations poses a risk to the genetic diversity of the wild populations. Currently there is little evidence that spring chinook released from Leavenworth or Entiat National Fish Hatcheries stray in substantial numbers to natural spawning areas (see section 2.6). Spring chinook released from Winthrop NFH do stray in substantial numbers to natural spawning areas in the Methow River, but the Winthrop NFH is in the process of phasing out their use of the Carson derived stocks and switching to the use of Methow-origin spring chinook.

Interim recovery level: The Upper Columbia River spring chinook populations must be naturally self-sustaining and not dependent on artificial propagation. Levels of gene flow from out-of-ESU hatchery stocks into natural Upper Columbia spring chinook populations should be less than 1% (McElhany et al. 1999), and patterns of straying and gene flow among the natural populations should be free from human-caused alterations.

³ The primary broodstock used by Carson NFH (Wind R) originated with collection in 1958 of spring chinook passing Bonneville Dam. The majority of these fish were probably returning to spawning grounds in the Snake River Basin, although other stocks from rivers in the upper and middle Columbia rivers also significantly contributed to the broodstock (Hymer et al. 1992).

5 Steelhead: Interim recovery goals

5.1 Number of populations

Current status: For the last several decades most steelhead spawning in the Upper Columbia River area have probably been part of a single population (see section 2.8.2). Spawners from this population are distributed in the Wenatchee, Entiat, Methow River basins. Very limited spawning also occurs in the Okanogan River basin.

Interim recovery goal: We suggest that a reasonable interim recovery level is three independent, viable populations, one each in the Wenatchee, Entiat and Methow Rivers basins. It is possible that the final recovery goals will also require a population of steelhead in the Okanogan, but we defer discussion of goals for steelhead in the Okanogan to an Upper Columbia River recovery team.

Having at least three populations will reduce the probability that a single catastrophic event could cause the extinction of the entire ESU. Multiple populations within an ESU will also increase the likelihood that a diversity of phenotypic and genotypic characteristics will be maintained. This will allow for the operation of natural evolutionary processes important for the long-term persistence of the ESU.

We emphasize that even if past management actions have resulted in the creation of a single Upper Columbia River steelhead population (see discussion above), this does not preclude a recovered ESU from containing multiple independent populations. The population definition we are using in the document is based on demography, not genetics. This means that even if genetic differences between historical steelhead populations have been lost due to the GCFMP and subsequent large-scale artificial propagation programs, this loss of diversity does not preclude groups of steelhead from becoming demographically independent in the future. In fact, this process has already begun with the creation of a separate steelhead supplementation program for the Wenatchee River (NMFS and others 1998). Over time, demographically independent populations will diverge genetically to a greater or lesser degree, depending on the size of each population, the rate of gene flow among the populations, and degree to which local ecological differences select for alternative genotypes in each population.

5.2 Population abundance

In setting interim recovery abundance levels for Upper Columbia steelhead, we followed the same general approach as we laid out for spring chinook (Figure 3.4).

Historical spawning abundance

Estimates of past spawning escapements for Upper Columbia steelhead are shown in Figures 4.1 and 4.2. The spawning abundance estimates are based on dam counts, which do not allow for accurate estimates of abundance for individual populations (Appendix B). Instead, we had combined spawning abundance estimates for the Methow and Okanogan River populations (Figure 4.1) and for the Wenatchee and Entiat River populations (Figure 4.2). The estimated geometric mean spawning population size for the combined Methow/Okanogan River populations from 1976 to 1996 was 1,928, and for the combined Wenatchee/Entiat River populations was 2,373. Over this same time period, the proportion of the spawning population in the Methow/Okanogan populations that consisted of hatchery produced fish ranged from 99% to 78% (Appendix B). The percentage of hatchery spawners in the combined Wenatchee/Entiat populations ranged from 87% to 48% (Appendix B). Until hatchery-only harvest policies were put in place starting in 1987, in tributary harvest rates on adult steelhead ranged from 50-76% in the Methow/Okanogan populations, and from 9-50% in the Wenatchee/Entiat populations (Figure 4.3; Appendix B).

Figure 4.1 - Estimated steelhead spawners above Wells Dam (Methow and Okanogan Rivers) (see Appendix B)

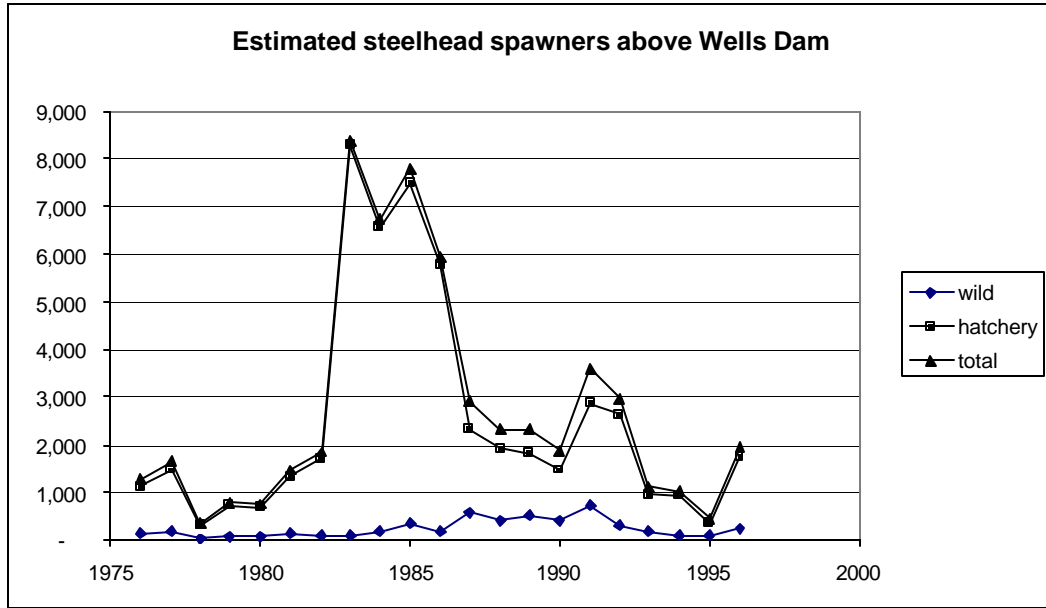


Figure 4.2 - Estimated steelhead spawners in the Wenatchee and Entiat Rivers (see Appendix B)

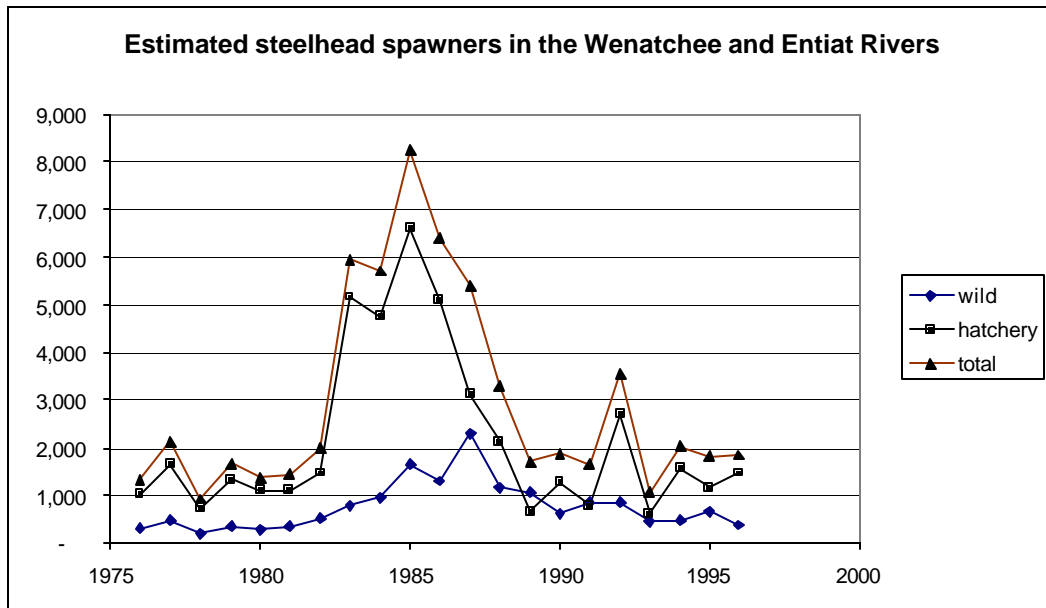
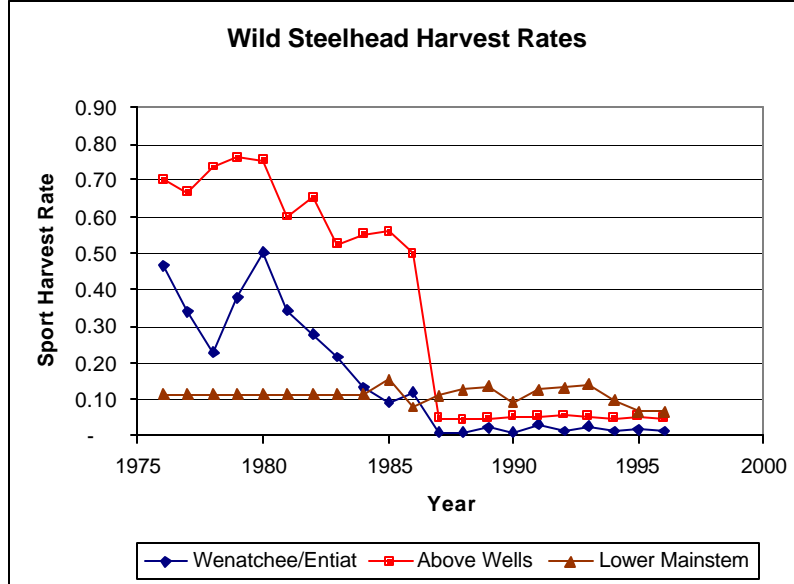


Figure 4.3 - Estimated harvest rates on wild Upper Columbia River steelhead (see Appendix B)



Estimates of current spawning and rearing habitat capacity

We obtained estimates of habitat capacity for steelhead from several sources, including spawner:recruit models, empirical relationships between habitat area and smolt numbers, and estimates of smolts passing Rock Island Dam (Appendix B; Table 4.1).

Table 4.1 - Steelhead habitat capacity

	Wenatchee	Entiat	Methow
Estimates based on spawners¹			
Mullan et al. (1992) Ricker Curve MSY estimates	2,275	417	2,212
Mullan et al. (1992) Beverton-Holt MSY estimates	3,307	606	3,213
Estimates of smolt capacity²			
Mullan et al. (1992) HQI smolt production	49,146-107,601	9,003-19,711	47,769-104,586
Adult equivalents for Mullan et al. estimates (3.0% smolt-adult survival)	1,474-3,288	270-591	1,433-3,137
Adult equivalents for Mullen et al. estimates assuming 66 smolts/spawner	744-1,630	136-299	723-1,585
Chapman smolt capacity estimates based on effective drainage area (81 smolts/sq. mi.)	114,372	23,895	137,781
Adult equivalents for Chapman estimates (3.0% smolt-adult survival)	3,431	717	4,133
Adult equivalents for Chapman estimates assuming 66 smolts/spawner	1,733	362	2,088
GAFM estimates (in Mullan et al. 1992)	100,000	22,300	58,552
GAFM2 estimates (WDFW unpub.)	62,167	12,739	35,113
Adult equivalents for GAFM estimates	3,000	669	1,757

(3.0% smolt-adult survival)			
Adult equivalents for GAFM2 estimates (3.0% smolt-adult survival)	1,865	382	1,053
Adult equivalents for GAFM estimates assuming 66 smolts/spawner	1,515	338	887
Adult equivalents for GAFM2 estimates assuming 66 smolts/spawner	942	193	532
Estimates of natural smolts at Rock Island Dam, apportioned to watersheds by effective drainage area	99,763	20,842	120,182
Adult equivalents at 3.0% smolt-adult survival	2,993	625	3,605
Adult equivalents at 66 smolts/spawner	1511	315	1921

1. Estimates from Appendix H in Mullan et al. (1992). Spawner:recruit models were fitted to the Upper Columbia River area as a whole, then apportioned into the three major tributaries based on smolt abundance (Table 8 of Appendix H of Mullan et al. (1992)).

2. Smolt capacity- Mullan et al. (1992) reported values (Appendix H, Table 8) for HQI smolt capacity estimates. Don Chapman suggested an approach based on effective drainage area, defined as the area upstream from the lower limit of rearing by stream annulus salmon and steelhead, basically the area above water where the daily maxima reach 22°C. Chapman calculates the Wenatchee, Entiat and Methow basins have 1412, 295, and 1701 m² of effective drainage, respectively. He then calculated the yield of smolts per square mile of effective drainage for the Snake basin during the mid-60's, a period considered to be full seeding, arriving at 81 steelhead smolts/mi². Mullan et al. (1992) also report values based on the Gradient Area Flow Model (GAFM) (also Appendix H, Table 8). GAFM2 values are GAFM values corrected for juvenile age structure (L. Brown, WDFW). GAFM2 values were computed directed only for the Wenatchee and Entiat basins; the value for the Methow basin was calculated by multiplying the GAFM values by 0.60, which was the mean of GAFM2/GAFM values for the Wenatchee (0.62) and the Entiat (0.57). The estimates of natural smolts at Rock Island dam is the average of the estimates from 1985 to 1998, and was obtained by a Peterson method as described by Peven and Hayes (1989) and Appendix B. The value of 3.0% smolt-adult survival is a mean of values in Mullan et al.(1992), and the estimate of 66 smolts/spawner was obtained by Tom Cooney (Appendix B). The estimates generated by the GAFM and GAFM2 models roughly correspond to maximum sustained yield seeding levels. They are not estimates of full carrying capacity.

Recommended interim recovery abundance levels:

In recommending interim recovery abundance levels for Upper Columbia steelhead, we used the same approach as we used for spring chinook salmon (Figure 3.4). Note that although we have provided interim recovery abundance levels for each population, we recognize that it may not be possible to accurately estimate spawning abundance at the scale of individual populations (see Appendix B). As we discussed earlier, native non-anadromous *O. mykiss* that spawn in Upper Columbia areas accessible to anadromous fish are considered part of the same biological ESU as Upper Columbia steelhead (Busby et al. 1996). Due to considerable uncertainty about the demographic relationships between resident and anadromous fish, however, we have not included resident fish in any of the spawning abundance levels we discuss below.

Wenatchee and Methow River populations - We recommend an interim recovery abundance level of ~2500 naturally produced spawners each for the Wenatchee and Methow Rivers. These abundance levels fall within a range defined by reasonable combinations of estimated smolt production capacities and smolt/spawner ratios, historical production levels and general conservation guidelines.

Entiat River population - We recommend an interim abundance recovery level for the Entiat River population of ~500 naturally produced spawners. This is considerably below the general conservation guidelines of several thousand spawners, but is consistent with estimates of current and historical habitat capacity.

Incorporating uncertainty - In order to be considered recovered, an Upper Columbia steelhead population must have a geometric mean naturally produced abundance significantly greater than its recovery level, measured over at least 12 years. We did not attempt to use the past variance in estimated abundance as an indicator of the likely future variance (like we did for spring chinook) because the demographic history of

these populations has been so dominated by artificial propagation that the assumption that the future variance in abundance will be similar to the past is untenable. We chose 12 brood cycles as a reasonable value over which to measure the geometric mean abundance because this roughly corresponds to two complete Upper Columbia steelhead generations, and is consistent with the range of time frames suggested by the spring chinook salmon uncertainty analyses.

Lower abundance thresholds

We recommend that the absolute and quasi-extinction criteria for Upper Columbia steelhead populations be the same as they are for the spring chinook populations. For all populations, absolute extinction is defined as one or fewer spawners in five consecutive years. For the Methow and Wenatchee River populations, we recommend quasi-extinction thresholds of 50 or fewer spawners per year for five consecutive years, and 30 or fewer spawners per year for five or more consecutive years for the Entiat River population. The long history of artificial propagation of Upper Columbia steelhead makes it impossible to come up with reasonable 'cautionary' thresholds, as we did for spring chinook salmon.

5.3 Population growth rate

Current status: We used historical dam count data to estimate historical natural return rates for the combined Methow/Okanogan and Wenatchee/Entiat River populations (Appendix B; Figures 4.5 and 4.6). The NRR's for Upper Columbia River populations have been estimated to be less than 1.0 for the entire time series for which data are available. The estimated NRR's for the Wenatchee/Entiat River populations are considerably higher than the estimated NRR's for the Methow/Okanogan River populations. These estimates indicate that the Upper Columbia River steelhead populations are not able to sustain themselves naturally at their observed abundance levels, although it is not clear from these data alone whether or not the Upper Columbia steelhead populations would go extinct without continual supplementation by hatchery fish. This uncertainty is due to questions about the relative reproductive success of naturally spawning hatchery fish, and the form of density dependence operating on Upper Columbia steelhead populations. Some of these issues may be resolved by more detailed modeling and/or experimentation.

Interim recovery criteria: In order to be considered recovered, an Upper Columbia steelhead population must have a geometric mean NRR significantly greater than 1.0, measured over 12 brood cycles. We did not attempt to use the past variance in estimated NRR as an indicator of the likely future variance (like we did for spring chinook) because the demographic history of these populations has been so dominated by artificial propagation that the assumption that the future variance in NRR will be similar to the past is untenable. We chose 12 brood cycles as a reasonable value over which to measure the NRR because this roughly corresponds to two complete Upper Columbia steelhead generations, and is consistent with the range of time frames suggested by the spring chinook salmon uncertainty analyses.

The criterion above assumes that the population will grow from a small size to its recovery level without substantial supplementation. Another scenario (perhaps more realistic for Upper Columbia River steelhead) that might lead to recovery would be to increase the population's size artificially via supplementation, and then stop supplementing when the population is large. If the population sustains itself after supplementation ceases, the population's geometric mean NRR would be equal to ~1 (after supplementation), but might never be significantly greater than 1. Under this scenario, a reasonable interim recovery criteria might be to require that the population's geometric mean NRR not be significantly less than 1.0, with the geometric mean calculated over a sufficient number of years to achieve a desired level of statistical power.

Figure 4.5 - Estimated Natural Return Ratios for Methow/Okanogan River steelhead populations

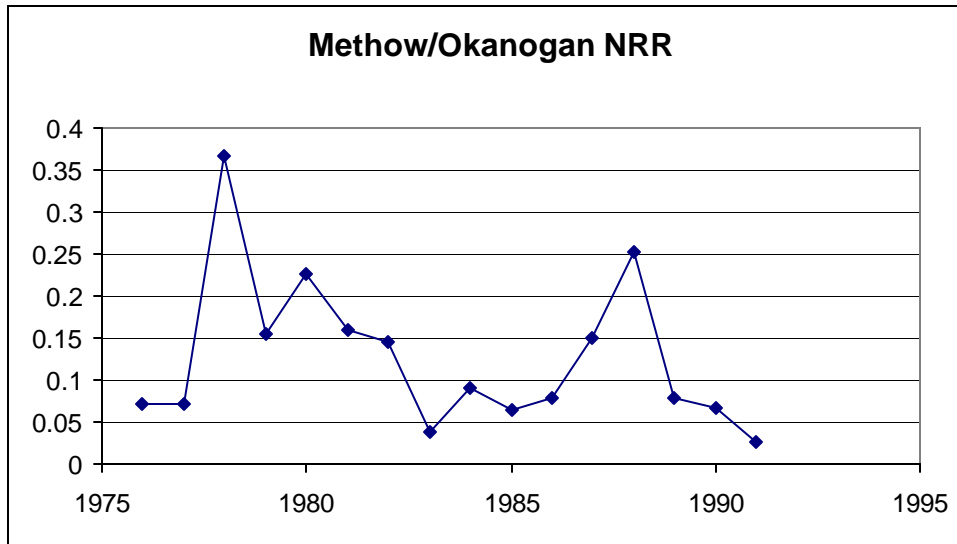
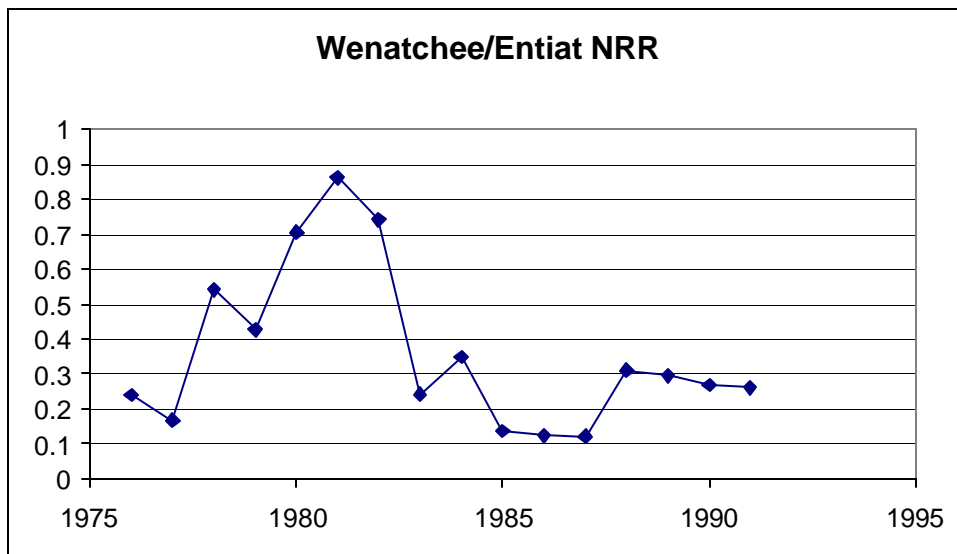


Figure 4.6 - Estimated Natural Return Ratios for the Wenatchee/Entiat River steelhead populations



5.4 Population structure

Current status: We have little information on the current status of substructure within Upper Columbia steelhead populations. It is likely that much of this substructure has been altered due to the large scale artificial propagation programs that have occurred over the last several decades.

Interim recovery level: In order to be considered recovered, Upper Columbia steelhead populations should be able to utilize properly functioning habitat in multiple spawning streams within each major tributary, with patterns of straying among these areas free from human-caused disruptions. At this time, we do not

believe that there is sufficient information on Upper Columbia steelhead spawning distributions to recommend any quantitative criteria for spawning distributions within each major tributary.

5.5 Diversity

Current status: Patterns of diversity within and among Upper Columbia steelhead populations have probably been substantially affected by large scale artificial propagation programs starting with the GCFMP in the late 1930's (Chapman et al. 1994). Patterns of diversity among populations were almost certainly affected by the practice of collecting broodstock at a central location (e.g., Rock Island Dam for the GCFMP, or Priest Rapids or Wells Dam for more recent programs) and then distributing the progeny of these broodstock throughout the Upper Columbia River area. These homogenizing effects would be exacerbated by the near elimination of naturally produced steelhead (Figures 4.1 and 4.2). Patterns of intrapopulation diversity were probably also substantially affected by artificial propagation. For example, the spawning timing distribution of Wells Hatchery is considerably earlier than naturally produced Upper Columbia steelhead. The fitness consequences of this change is not known, but if patterns of diversity in natural populations reflect some to degree of adaptation to natural conditions, then artificially altering these patterns of diversity is unlikely to be beneficial to the populations in the wild. The genetic basis of traits such as spawn timing are not well understood and the degree to which changes in patterns of phenotypic diversity of Upper Columbia steelhead reflect genotypic changes is not known at this time. Based on what is known experimentally about the heritability of phenotypic traits in salmonids, it is likely that selection for traits such as spawn timing will usually produce at least some heritable response (reviewed by Tave (1993)).

Interim recovery criteria: The Upper Columbia River steelhead populations must be naturally self-sustaining and not dependent on artificial propagation. Levels of gene flow from out-of-ESU hatchery stocks into natural Upper Columbia steelhead populations should be less than 1%, and patterns of straying and gene flow among the natural populations should be free from human-caused alterations.

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